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CRYPTANTHA OF SOUTHERN CALIFORNIA

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ABSTRACT: The genus *Cryptantha* (Boraginaceae) contains 202 species, with 49 species and 56 taxa (including varieties) occurring in Southern California, defined here as including the entire Southwestern California region and Tehachapi Mountain region of the California Floristic province, the entire Desert province, and most of the White and Inyo Mountain subregion of the Great Basin province. The purposes of this article are 1) to summarize the current taxonomy of *Cryptantha* species and infraspecies in Southern California; 2) to provide taxonomic keys and images illustrating the diagnostic features for identification; and 3) to review the distribution, environmental factors, and current conservation status of these taxa.

KEYWORDS: *Cryptantha*, Boraginaceae, taxonomy, identification.

INTRODUCTION

Taxonomic History and Nomenclature

Cryptantha Lehmann ex G. Don, commonly known as “popcorn flower” or “cat’s eye,” is a genus within the family Boraginaceae. The circumscription of this family has changed repeatedly over the last twenty years [Engler and Prantl 1897, Heywood et al. 2007, Gottschling *et al.* 2001, Angiosperm Phylogeny Group (APG II) 2003], with various authors recognizing either a broad or narrow family concept. Here we accept the APG II (2003) system of classification, which recognizes a broad Boraginaceae. As treated in this manner, the family may be divided into subfamilies Boraginoideae, Cordioideae, Eretioideae, Heliotropoideae, Hydrophyllloideae, and (possibly) Lennoideae (see Stevens 2001 onwards). Despite these changes in classification, *Cryptantha* firmly belongs in subfamily Boraginoideae, characterized by an inflorescence that is a scorpioid cyme (Buys and Hilger 2003), a deeply 4-lobed ovary with a gynobasic style, and a fruit that is a schizocarp of nutlets.

Cryptantha is an amphitropically distributed genus, with taxa in both western North America and western South America, but lacking populations in between. The genus is currently catalogued at 202 species. The greatest species diversity, 136 species, occurs in western North America, with distributions from Alaska to southern Mexico, and

as far east as Texas (Johnston 1925; Payson 1927; Higgins 1971; Mabberley 2008). Approximately 69 species occur in western South America, in Peru, Chile, Bolivia, and east to Argentina (Reiche 1915; Johnston 1927; Schwarzer 2007; Zuloaga et al. *in prep*). Three species, *C. albida*, *C. circumscissa*, and *C. maritima*, are distributed in both North and South America.

Members of the genus are annual, biennial, or perennial herbs. Stems are simple to highly branched, generally ascending to erect, and densely covered in trichomes (Johnston 1925; Payson 1927; Munz and Keck 1959, 1968; Higgins 1971; W.A. Kelley and Wilken 1993, Mabberley 2008; R.B. Kelley *in prep*). Often in perennial taxa, a basal rosette of robust leaves is present before and during inflorescence growth. Among annuals, the basal rosette is common early in development but is lost as the internodes of the aerial shoots (including inflorescence) elongate. Cauline leaves range from opposite to alternate in arrangement. Leaf shape is spatulate, lanceolate, oblanceolate, but most often linear. Leaves have acute to obtuse bases. Leaf vestiture is strigose, “rough hairy,” or “bristled.” The largest, relatively stout trichomes, which are often designated as bristles, often have bulbous bases, described as pustulate (giving a tessellate appearance to the leaf surface). These pustules are composed of epidermal cells arranged in a ring around the trichome base; the epidermal cells are elevated, opaque, and silicified and are thought to be cystolith in origin (Johnston 1925). The trichomes are most often translucent and white, but can be yellow-brown in some taxa. The inflorescence is characteristic of subfamily Boraginoideae, being a circinate (coiled), scorpioid cyme unit (often described as a helicoid cyme, but see Buys and Hilger 2003); however, the inflorescence structure is often obscured by short internodes and absence of floral bracts. The calyx, considered part of the fruiting unit, is accrescent, and continues to grow as the nutlets mature. The shape and fusion of the calyx, as well as calyx vestiture and orientation when the plant is in fruit, varies among taxa and is often used to distinguish them. Flowers are **chasmogamous** (opening and capable of cross-pollination) in most taxa, but may be **cleistogamous** (not opening and self-pollinated) in members of subgenera *Cryptantha* and *Geocarya* (modified into lenticular structures in the last). The corolla **limb** (the expanded portion above the corolla tube, containing the five lobes) ranges in size from less than 1 mm wide (measured across from lobe to lobe) to up to 2 cm wide. Corollas are almost universally white (a few species having yellow corollas), and are rotate to salverform. The corolla tube is usually equal to the calyx in length and bears five epipetalous stamens. At the outer corolla throat, the tissue is invaginated, resulting in five pinched or folded regions, known as **forrices**. The forrices, which enclose the throat, can vary in size, shape, and color, but are often yellow and possibly function as nectar guides. Corolla lobes are ovate-oblong or suborbicular, ranging from widely spreading to ascending in chasmogamous species. As is characteristic of the subfamily Boraginoideae, the ovary is deeply four-lobed, with a **gynobasic style** arising from the base and center of the ovary lobes. The ovary lobes mature into 1-seeded units with hardened pericarps, termed **nutlets**. The number of nutlets that develop to maturity can vary from 1 to 4. The tissue between the ovary lobes, interpreted as either receptacular tissue or the style base, continues to elongate and differentiate during fruit maturation. This tissue

is often called the **gynobase** and is that to which the nutlets are laterally attached at maturity. The gynobase is generally narrowly-pyramidal in form, elongating during fruit maturation. (Note that “fruit” is used here to include the nutlets and accompanying calyx.) Nutlets are generally ovate to lanceolate in shape. The fruits of annual taxa are generally deciduous, and the whole unit encased by the calyx will easily detach from the inflorescence; however, in the perennial subgenus *Oreocarya*, the nutlets detach easily but the calyx and pedicel remain firmly attached to the plant. Several annual species in North American have fruits comprised of heteromorphic nutlets. Often, there are three smaller, easily detached nutlets, and one larger nutlet that is strongly adnate to the gynobase. The pericarp wall is variable in sculpturing and color. The attachment scar is generally a shallow, triangular areole (generally not rimmed or elevated), which is continuous with the ventral groove. When describing the ventral groove, morphologists generally consider the groove and attachment scar as one feature on the nutlet; thus the ventral groove is often described as being basally forked.

The genus name *Cryptantha* was first used by Johann Georg Christian Lehmann in a seed catalogue for the Hamburg Botanical Garden. In 1836, Fischer and Meyer used Lehmann’s proposed name *Cryptantha* in association with two South American species, *C. glomerata* and *C. microcapa*, but with no formal genus diagnosis. In that same year, however, the name *Cryptantha* was validly published in the *General System of Gardening and Botany* by Don (1836), who provided the first formal diagnosis for the genus in association with the same two South American species (Johnston 1925). Thus, authorship of the genus should correctly be cited as *Cryptantha* Lehmann ex G. Don. Greene (1887a,b,c) was the first botanist to carefully study the borages of tribe Eritrichieae (within which *Cryptantha* has been classified), which are diverse in western North America. He authored several revisions of Eritricheae members, including *Cryptantha*, in a series of papers in the journal *Pittonia*. Greene recognized the importance of classifying the group based on characters other than floral appearance, noticing the great variation in nutlet characteristics among members of this tribe. He expanded the genus *Cryptantha* to include North American species that had been placed in the genus *Krynitzkia* Fisch. & C.A. Mey. Greene’s circumscription of *Cryptantha* included strictly annual taxa with deciduous fruits. Additionally, Greene recognized several genera that are now treated as part of *Cryptantha*, including *Oreocarya* Greene, *Piptocalyx* Torr. [= *Greeneocharis* Gürke & Harms], and *Eremocarya* Greene. The next major revision came in the dissertation research of the Boraginaceae expert I. M. Johnston in 1925. In this monographic treatment of the North American species of *Cryptantha*, the genus was circumscribed to include *Eremocarya* and *Piptocalyx* [= *Greeneocharis*]. Each species was revised and clarified in this work, with each of the 57 species placed into one of fifteen sections. Shortly after the publication of his dissertation, Johnston spent several months in South America. These studies, with new herbarium vouchers, led Johnston to conclude that the perennial *Oreocarya* species should also be included in *Cryptantha* to form one large, homogenous genus. In 1927, Johnston published treatments of South American Boraginaceae, recognizing *Cryptantha* as having three subgenera in South America: *Krynitzkia*, *Geocarya*, and *Eucryptantha* [= *Cryptantha*]. Also in 1927, Payson, who was working on a

Table 1. Subgenera of *Cryptantha* recognized by Johnston (1927) and Payson (1927).

| Subgenus | Characters delineating subgenus |
|---|---|
| <i>Eucryptantha</i> [= <i>Cryptantha</i>] | Plants with cleistogamous flowers. Cleistogamous flowers similar to chasmogamic flowers, except for closed corolla. Cleistogamous flowers located in axiles of leaves and often throughout the inflorescence. Distributed in South America. |
| <i>Geocarya</i> | Plants with cleistogamous flowers. Basal cleistogamous flowers highly specialized into lenticular structures. Distributed in South America. |
| <i>Krynitzkia</i> (incl. <i>Eremocarya</i> and <i>Greeneocharis</i>) | Annual plants having only chasmogamous flowers. Distributed in North and South America. |
| <i>Oreocarya</i> | Perennial or biennial herbs, producing only chasmogamous flowers. Restricted to North America. |

monograph of *Oreocarya*, agreed with Johnston that *Oreocarya* should be included in *Cryptantha*. Payson, following Johnston’s treatments, recognized four subgenera in *Cryptantha*: *Oreocarya*, *Krynitzkia*, *Geocarya* and *Eucryptantha* [= *Cryptantha*]. (See Table 1 for details of the characters used to circumscribe these subgenera, and their distributions.) Since the 1920s, systematists have made revisions among species and their relationships within *Cryptantha*, but the subgenera themselves have remained largely unchanged. Higgins, another expert on the perennial taxa, published a revised monograph of *Oreocarya* in 1971, and agreed with Johnston and Payson on the inclusion of *Oreocarya* within *Cryptantha*. However, the classification of *Oreocarya* has been contentious. For example, Abrams (1951) recognized *Oreocarya* as genus separate from *Cryptantha* in his *Illustrated Flora of the Pacific States: Washington, Oregon and California*. More recently, Weber (1987) also recognized *Oreocarya* at the genus level, giving no specific reason for his circumscription, but arguing that genera should consist only of species easily recognizable by suites of characters. However, most recent classifications follow the treatments of Johnston, Payson, and Higgins in circumscribing *Cryptantha* in the broad sense, as encompassing all four subgenera. For Southern California, these include the treatments of *Cryptantha* in Munz (1974), *The Jepson Manual* (W.A. Kelley and Wilken 1993), and the draft treatment for the second edition of *The Jepson Manual* (R.B. Kelley in prep).

Hasenstab (2009), in a molecular phylogenetic analysis of *Cryptantha* and relatives, concluded that the genus *Cryptantha* as currently defined appears to be paraphyletic, warranting the resurrection of several genera, including *Eremocarya*, *Greeneocharis*, and *Oreocarya*. Although we feel it premature to divide the genus for this article, the key we have prepared reflects (in part) a more natural grouping of taxa.

Definition of the Southern California Region

As this article is on the *Cryptantha* of Southern California, we must define what we mean by that geographic designation. We use Munz’s concept of Southern California, as he recognized it in *A Flora of Southern California* (1974). He defined the northern boundary of Southern California as “Point Conception, eastward along the crest of



Figure 1. Regions and provinces from *The Jepson Manual* (Hickman 1993), corresponding to Southern California, sensu Munz (1974). See this work for included subregions and districts.

the Santa Ynez mountains to the Mt. Pinos region in Ventura County, Fort Tejon in Kern County, the Tehachapi and Piute mountains, then northward to Little Lake in Inyo County and along the east slopes of the Inyo and White mountains to the Deep Springs region.” Munz stated that the region does not include the northern part of Santa Barbara County, the southern end of the San Joaquin Valley, nor any of the Owens Valley, as these regions contain more of a northern element of the flora (Figure 1).

This boundary for “Southern California” contains components of three floristic provinces designated in *The Jepson Manual* (Hickman 1993): 1) The entire Southwestern California region (including the South Coast, Channel Islands, Transverse Ranges, and Peninsular Ranges subregions) and the Tehachapi Mountain subregion of the California Floristic province; 2) the entire Desert province (Sonoran and Mohave deserts, including the Desert mountains); and 3) the White and Inyo Mountain subregion of the Great Basin province. Although “Southern California” is often viewed as a socio-political designation, the region as defined here actually corresponds to major floristic provinces, regions, or subregions of California and thus has some scientific meaning. With regard to county borders, Southern California includes all of San Diego, Imperial, Los Angeles, Orange, Riverside, Ventura, and San Bernardino counties, the extreme southern and southeastern portion of Santa Barbara County, the extreme southern, south-central, and eastern parts of Kern County, all except the extreme northwestern and a small northeastern part of Inyo County, and a southeastern swath of Mono county (Figure 1).

Identification of Southern California *Cryptantha*

Cryptantha species and infraspecies are generally recognized as being difficult to identify, even by professional botanists; the taxa are often being perceived to look very similar to one another. Perhaps the major reason for this perception is that the main feature used in identifying flowering plants – the flower itself – is generally both obscure and uniform among *Cryptantha* taxa. The corolla, the primary cue of identification both for humans and potential pollinators, is rarely used in *Cryptantha* identification, except for some variation in size and (rarely) in color. And yet, it should be pointed out that *Cryptantha* taxa vary tremendously in a great number of features, only some of which are listed in Table 2. Many of these features collectively contribute to the reflection of light, interpreted by our brains as a pattern. Thus, despite the variation among individual plants due to differences in habitat and developmental stage, it is possible, with practice, to recognize *Cryptantha* species at a glance (Figure 2A–D). This wholistic, pattern recognition method is how most botanists and hobbyists identify plants.

Until one develops a wholistic pattern recognition familiarity with *Cryptantha*, one must rely instead on analytic methods, especially taxonomic keys and diagnostic descriptions. Interestingly, relatively few of the characters listed in Table 2 are actually used in keys. Among these major features in identification are plant duration, branching pattern and position, bract presence, pedicel length, calyx length (in flower and fruit),

Table 2. Some characters used to distinguish between *Cryptantha* taxa, those in bold most often used in taxonomic keys.

| | |
|--|--|
| Plant duration | Calyx vestiture / trichome type |
| Stem type | Calyx posture |
| Stem vestiture / trichome type | Calyx orientation |
| Branch number / position | Corolla tube length |
| Internode length | Corolla limb width |
| Leaf position | Corolla color |
| Leaf size | Fornices color |
| Leaf shape | Gynobase size / shape |
| Leaf vestiture / trichome type | Style length |
| Inflorescence position | Nutlet number per fruit |
| Flower internode length | Nutlet size |
| Bract presence / morphology | Nutlet shape / base / margin / apex |
| Pedicle length | Nutlet sculpturing |
| Calyx length (flower vs. fruit) | Nutlet symmetry |
| Calyx / Sepal shape | Nutlet ventral groove shape |

calyx/sepal shape, calyx vestiture/trichome type, and corolla limb width (Table 2). However, variation in nutlet morphology is most important in *Cryptantha* identification, including nutlet number (per fruit), size, shape, and sculpturing. (Why nutlet variation is so great in this complex is a question of great interest regarding the evolution of the group.) Thus, it is critical to collect *Cryptantha* specimens at a stage when at least some mature fruits are present. Identification of immature plants can be quite problematic.

Observations of most of these key characteristics require the use of a good dissecting microscope and basic dissecting tools. In addition, we have found two procedures to be of value in identification of *Cryptantha* (and of related taxa, such as *Amsinckia*, *Pectocarya*, and *Plagiobothrys*). First, if nutlets adhere to and are difficult to remove from the gynobase, boiling the fruits for 1–2 minutes will usually loosen them, allowing them to be removed intact (Figure 2E). Second, to clearly see details of the fruits or calyx, it is valuable to place them on a glass microscope slide covered with a strip of double-stick tape and a label with herbarium voucher information (Figure 2F). Note that in order to get an accurate count of nutlet number, care must be taken both to choose fruits that are not too mature (i.e., before the nutlets or entire fruits have naturally fallen away) and to avoid dislodging nutlets prematurely during dissection.

MATERIALS AND METHODS

Herbarium specimens or live plants (subsequently vouchered) were photographed with a Nikon Coolpix 4400 or a Sony digital camera. Close-ups of vegetative parts, flowers, or fruits were photographed either using a Wild M3Z dissecting scope with a Nikon Coolpix 995 digital camera or using a Visionary Digital Imaging System (consisting of an FX2 lighting system, Infinity Optics Long Distance Microscope, SolMate trans-illuminator, Precision Linear Camera Controller, 10 megapixel digital camera, and a devoted computer workstation with Helicon Focus software). Appendix

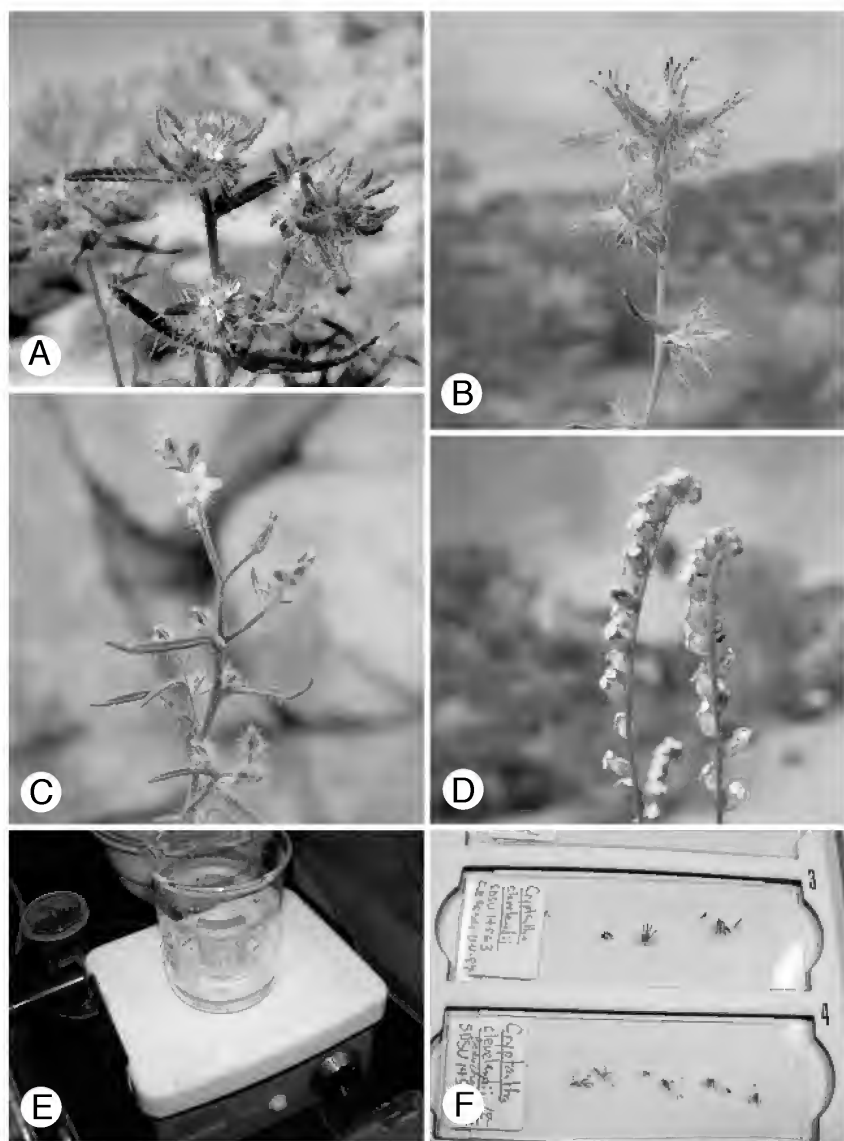


Figure 2. **A-D:** Species of *Cryptantha*, illustrating that many do look different and can be site-identified. **A:** *C. maritima*. **B:** *C. nevadensis*. **C:** *C. racemosa*. **D:** *C. utahensis*. **E:** Boiling of fruits for 1-2 minutes will loosen nutlets. **F:** Microscope slides with double-stick tape and labels for observing *Cryptantha* nutlets.

I lists herbarium voucher accessions for all *Cryptantha* images (except for a few field photographs), by figure number and letter. Dichotomous keys were modified from pre-existing keys from Munz and Keck (1959), Munz (1974), W.A. Kelley and Wilken (1993), and R.B. Kelley (*in prep*). For current nomenclature and descriptions, we are especially appreciative of an early version of R.B. Kelley's treatment of the genus for the upcoming second edition of *The Jepson Manual*. Information on bioregions was obtained from R.B. Kelley (*in prep*) and from W.A. Kelley and Wilken (1993). County and regional distributions were obtained from herbarium vouchers listed on the *Consortium of California Herbaria* (2009; see Rosatti 2003) for the region of Southern California as defined in this paper; however, identifications were not confirmed by us, except in a few cases. Information on sensitive or rare taxa was obtained from the California Native Plant Society Inventory (2009), cited in the text as a CNPS listing, both in descriptions and the **Conservation Status and Ecology of Southern California *Cryptantha*** section.

The following keys, plus multi-entry (polythetic) keys, numerous images, distribution maps, and nomenclatural information, are accessible at our *Cryptantha* web site: <http://www.sci.sdsu.edu/plants/cryptantha>. Our aim is to provide a service for both professionals and amateurs in the identification of this fascinating group of plants. We provide an initial key to previously recognized groups (variously treated in the past as subgenera or separate genera): *Eremocarya*, *Greeneocharis*, *Krynitzkia*, and *Oreocarya*. We do not include detailed descriptions of taxa, but these will be forthcoming in the second edition of *The Jepson Manual* (R.B. Kelley *in prep*). We cite only the diagnostic features of each taxon, its general and county distribution, pertinent ecological information, and conservation status, where applicable. Species diagnoses and plates appear in the order presented in keys and not in alphabetical order so as to more clearly illustrate and compare diagnostic features. For ease of use, each major group and individual taxa are numbered in the keys and descriptions. Technical terms that we use include **dorsal**, for the back side of a nutlet, i.e., the side facing away from the gynobase, and **ventral**, for the inner side of a nutlet, facing the gynobase. (See *Cryptantha* web site: *Keys* for a complete list of terminology and their definitions.) Corolla width is always measured from lobe to lobe of the **corolla limb**, the expanded portion at the apex of the tube or throat. We do not include distribution maps (due to space concerns), but encourage all to do a specimen search for selected taxa on the *Consortium of California Herbaria*.

KEYS TO *CRYPTANTHA* OF SOUTHERN CALIFORNIA

The 49 species and 56 taxa (including varieties) of *Cryptantha* occurring in Southern California are listed in Table 3. The initial key, below, segregates taxa into “groups” that correspond to previously recognized genera or subgenera. The *Krynitzkia* group is further divided into two keys: one for smooth nutlets and one for rough nutlets.

Table 3. The 49 species and 56 taxa of *Cryptantha* in Southern California. Taxonomy after R. B. Kelley, in prep. *= *Eremocarya*; ** = *Greeneocharis*; *** = *Oreocarya*; all others “*Krynitzkia*”. CNPS Inventory listings in **bold**.

| | | |
|--|---|---|
| <i>C. affinis</i> | <i>C. gracilis</i> | <i>C. nubigena</i> *** |
| <i>C. angustifolia</i> | <i>C. hoffmannii</i> *** | <i>C. oxygona</i> |
| <i>C. barbigera</i> var. <i>barbigera</i> | <i>C. holoptera</i> 4.3 | <i>C. pterocarya</i> var. <i>cycloptera</i> |
| <i>C. barbigera</i> var. <i>fergusoniae</i> | <i>C. humilis</i> *** | <i>C. pterocarya</i> var. <i>pterocarya</i> |
| <i>C. cinerea</i> var. <i>abortiva</i> *** | <i>C. inaequata</i> | <i>C. pterocarya</i> var. <i>purpusii</i> |
| <i>C. circumscissa</i> var. <i>circumscissa</i> ** | <i>C. intermedia</i> var. <i>intermedia</i> | <i>C. racemosa</i> |
| <i>C. clevelandii</i> var. <i>clevelandii</i> | <i>C. leiocarpa</i> | <i>C. recurvata</i> |
| <i>C. clevelandii</i> var. <i>florosa</i> | <i>C. lepida</i> * | <i>C. roosiorum</i> *** 1B.2 |
| <i>C. clokeyi</i> 1B.1 | <i>C. maritima</i> var. <i>maritima</i> | <i>C. scoparia</i> 4.3 |
| <i>C. confertiflora</i> *** | <i>C. micrantha</i> * | <i>C. similis</i> ** |
| <i>C. corollata</i> | <i>C. micromeres</i> | <i>C. simulans</i> |
| <i>C. costata</i> 4.3 | <i>C. microstachys</i> | <i>C. sparsiflora</i> |
| <i>C. decipiens</i> | <i>C. mohavensis</i> | <i>C. torreyana</i> |
| <i>C. dumetorum</i> | <i>C. muricata</i> var. <i>denticulata</i> | <i>C. traskiae</i> 1B.2 |
| <i>C. echinella</i> | <i>C. muricata</i> var. <i>jonesii</i> | <i>C. tumulosa</i> *** 4.3 |
| <i>C. flaccida</i> | <i>C. muricata</i> var. <i>muricata</i> | <i>C. utahensis</i> |
| <i>C. flavoculata</i> *** | <i>C. nemaclada</i> | <i>C. virginensis</i> *** |
| <i>C. ganderi</i> 1B.1 | <i>C. nevadensis</i> var. <i>nevadensis</i> | <i>C. watsonii</i> |
| <i>C. glomeriflora</i> 4.3 | <i>C. nevadensis</i> var. <i>rigida</i> | |

Key to *Cryptantha* Groups

- 1. Plants annual, gen wider than tall, often rounded to cushion-like; taproot red or purple when dry (often staining herbarium paper); flower bracts present
 - 2. Calyx basally fused, tubular, tube circumscissile in fruit **Group 1: *Greeneocharis*, p. 11**
 - 2' Calyx of distinct sepals, intact in fruit **Group 2: *Eremocarya*, p. 13**
- 1' Plants annual, biennial, or perennial, gen taller than wide, rarely rounded to cushion-like; taproot usually not red or purple when dry; flower bracts absent or rarely present
 - 3. Plants biennial or perennial; vegetative leaves basal or tufted; nutlets smooth, rugose, or scabrous, apically broadly rounded to obtuse; ventral groove apex well below nutlet apex **Group 3: *Oreocarya*, p. 13, 15**
 - 3' Plants annual or rarely perennial; vegetative leaves cauline; nutlets smooth, papillate, tuberculate, or muricate, apically narrowly acute to acuminate; ventral groove apex almost to nutlet apex **Group 4: *Krynitzkia*, p. 20**

Group 1: *Greeneocharis* [*Piptocalyx*]

The two species of *Greeneocharis* (named after Edward Lee Greene, 1843-1915) are readily distinguished by the combination of red to purple-pigmented roots, bracteate flowers, and a calyx that is basally synsepalous (sepals fused), splitting transversely at fruit maturity, a condition termed **circumscissile dehiscence**. Interestingly, the only other close relatives with such a calyx dehiscence are two species of *Plagiobothrys*: *P. arizonicus* and *P. nothofulvus*. See Figures 29A,B for comparative nutlet images in the *Greeneocharis* group.

1. Corolla 1–2 mm wide, fornices tiny, white 1. *C. circumscissa* var. *circumscissa*
 1' Corolla 3–6 mm wide, fornices evident, yellow 2. *C. similis*

1. *Cryptantha circumscissa* var. *circumscissa* (Hook. & Arn.) I.M. Johnst.

(Figure 3A-E, p.12)

Common name: Circumscissile cryptantha. **Distribution in Southern California:** Southwestern California region (eastern South Coast, Transverse Ranges, and eastern Peninsular Ranges), Desert province, White and Inyo mountains; Imperial, Inyo, Kern, Los Angeles, Mono, Riverside, Santa Barbara, San Bernardino, San Diego, and Ventura counties. **Conservation Status:** None. **Diagnosis:** Plants (at maturity) generally wider than tall with red-purple roots and bracteate flowers, distinguished from the *Eremocarya* group in having circumscissile calyces and from *C. similis* by the smaller (1-2 mm wide) corolla. **Note:** *C. circumscissa* var. *rosulata*, the ground rose cryptantha (CNPS 1B.2 listing), has a limited distribution in subalpine habitats of the Sierra Nevada, Inyo and Tulare Cos., outside Southern California.

2. *Cryptantha similis* K. Matthew & P.H. Raven

(Figure 3F-J, p.12)

Common name: Dome cryptantha. **Distribution in Southern California:** Southwestern California region (northern San Gabriel and western San Bernardino mountains), southwestern Mohave Desert region; Kern, Los Angeles, and San Bernardino counties. **Conservation Status:** None. **Diagnosis:** Plants (at maturity) generally wider than tall with red-purple roots and bracteate flowers, distinguished from the *Eremocarya* group in having circumscissile calyces and from *C. circumscissa* by the larger (3-6 mm wide) corolla. [*C. circumscissa* (Hook. & Arn.) I.M. Johnst. *in part*, sensu W.A. Kelley and Wilken 1993]

These two taxa are distinguished only by corolla size and color of fornices. The range of *Cryptantha similis* is much more restricted, but appears to overlap, with that of *C. circumscissa*.

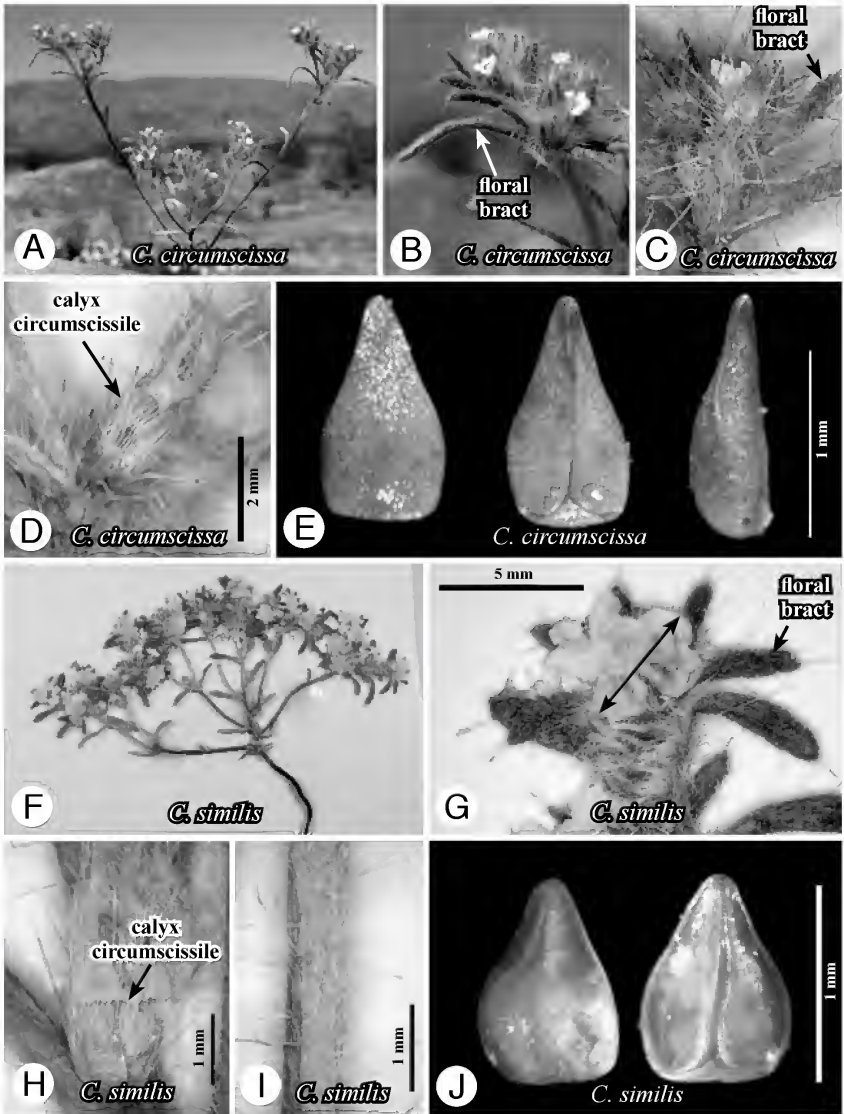


Figure 3. A-E: *Cryptantha circumscissa*. **A:** Whole plant, showing small height relative to width. **B-C:** Inflorescence and flowers. Note bracts and small corolla. **D:** Circumscissile calyx. **E:** Nutlet, dorsal (left), ventral (middle), and lateral (right) views. **F-J: *C. similis*.** **F:** Whole plant. **G:** Flowering shoot. Note wide (3-6 mm) corolla and floral bracts. **H:** Circumscissile calyx. **I:** Stem close-up, showing appressed and spreading trichomes. **J:** Nutlet, dorsal (left) and ventral (right) views.

Group 2: *Eremocarya*

The two species of *Eremocarya* (from *eremo*, desert + *carya*, fruit) are distinguished by the combination of red to purple-pigmented roots, bracteate flowers, and an aposepalous calyx (sepals not fused). Thus, it is the latter feature that distinguishes this group from *Greeneocharis*. See Figures 29C,D for comparative nutlet images in the *Eremocarya* group.

1. Corolla limb 1–3.5 mm wide 3. *C. lepida*
 1' Corolla limb 0.5–1.2 mm wide 4. *C. micrantha*

3. *Cryptantha lepida* (A. Gray) I.M. Johnst. (Figure 4A-E, p.14)

Common name: Elegant cryptantha. **Distribution in Southern California:** Southwestern California region (Peninsular and Transverse Ranges), Desert province; Imperial, Kern, Los Angeles, Riverside, San Bernardino, San Diego counties. **Conservation Status:** None. **Diagnosis:** Plants (at maturity) generally wider than tall with red-purple roots and bracteate flowers, distinguished from the *Greeneocharis* group in having non-circumscissile calyces and from *C. micrantha* in having larger (1–3.5 mm wide) corollas. [*C. micrantha* (Torrey) I.M. Johnst. in part, sensu W.A. Kelley and Wilken 1993]

4. *Cryptantha micrantha* (Torrey) I.M. Johnst. (Figure 4F-J, p.14)

Common name: Purple Root cryptantha. **Distribution in Southern California:** mostly Desert province; Imperial, Inyo, Los Angeles, Riverside, San Bernardino, San Diego counties. **Conservation Status:** None. **Diagnosis:** Plants (at maturity) generally wider than tall with red-purple roots and bracteate flowers, distinguished from the *Greeneocharis* group in having non-circumscissile calyces and from *C. lepida* in having smaller (0.5–1.2 mm wide) corollas.

Note that some overlap occurs in the overall corolla width of these two species. However, within a plant, most flowers fit the range of their respective species. The two taxa also seem to occupy different habits, *C. lepida* in montane and desert transition regions, occasionally cismontane washes, and *C. micrantha* in lower elevation desert regions, generally flats and alluvial slopes, often sandy soils, with creosote bush scrub.

Group 3: *Oreocarya*

The species of *Oreocarya* (*oreo*, mountain + *carya*, fruit) are distinctive in being biennial or perennial taxa with a generally well formed and persistent rosette of leaves. Many of these taxa occur at high elevations. In addition, the nutlets in this group tend to be larger than other *Cryptantha* species, usually with characteristic rounded apices and ventral grooves that do not extend to the nutlet apex. See Figure 26 for comparative nutlet images in the *Oreocarya* group.

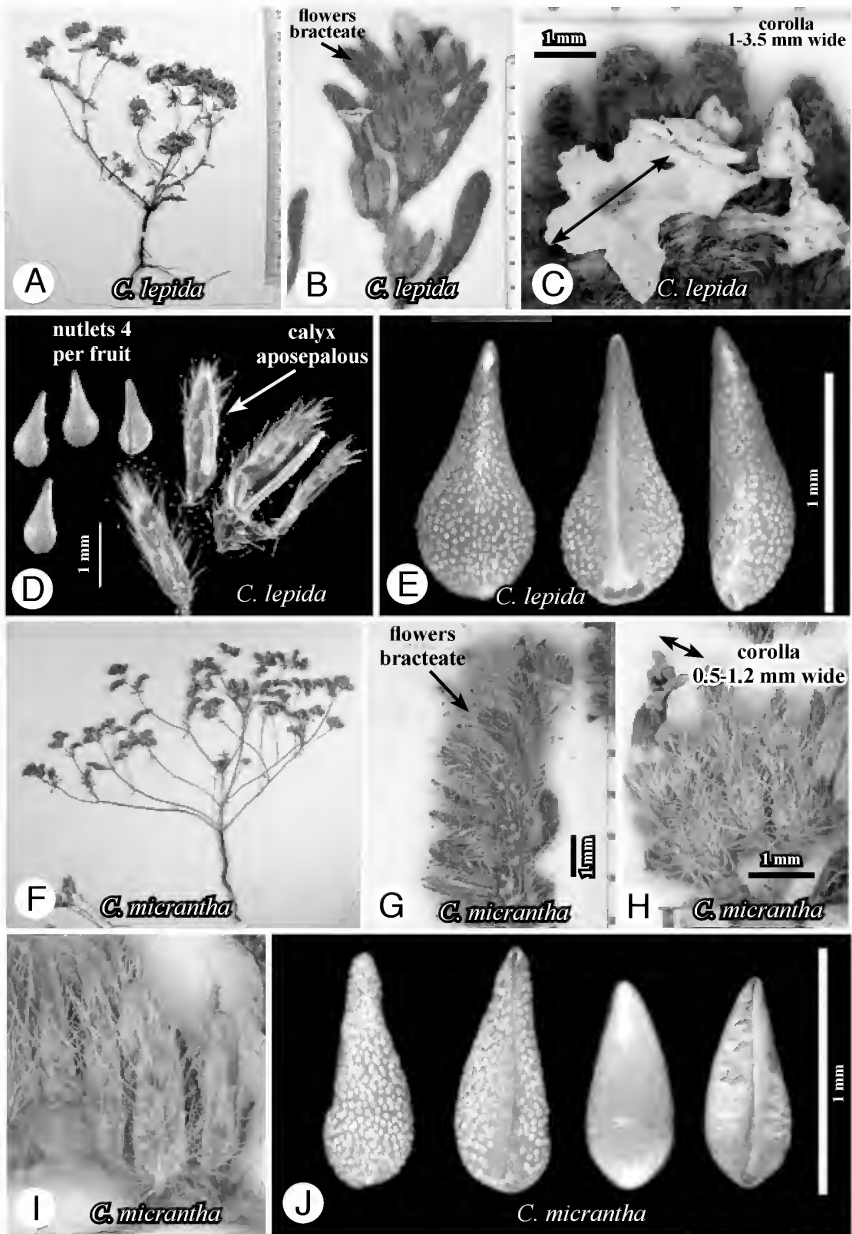


Figure 4. A-E: *Cryptantha lepida*. **A:** Whole plant. **B:** Inflorescence, note floral bracts. **C:** Flower, showing larger (1-3.5 mm wide) corolla. **D:** Fruit, with 4 nutlets removed; note unfused sepals (calyx aposepalous). **E:** Nutlet, dorsal, ventral, and lateral views (left to right). **F-J: *C. micrantha*.** **F:** Whole plant, wider than tall. **G:** Inflorescence, with floral bracts. **H:** Flower, showing small (0.5-1 mm wide) corolla. **I:** Fruit, with unfused sepals. **J:** Nutlets, two forms: rough (left, dorsal and ventral views) and smooth (right, dorsal and ventral views).

Key to *Oreocarya* Group

1. Corolla tube > sepals
 2. Corolla and fornices yellow; nutlet back smooth, groove closed, ventral groove margins \pm overlapping **5. *C. confertiflora***
 - 2' Corolla white, fornices light yellow; nutlet back rough, groove open, narrowed near middle, ventral groove margins elevated **6. *C. flavoculata***
- 1' Corolla tube = or < sepals
 3. Stems prostrate to ascending; nutlet dorsal side strongly convexly curved, surface smooth; groove closed, margins generally overlapping **7. *C. cinerea* var. *abortiva***
 - 3' Stems \pm erect (generally caespitose in *C. humilis*); nutlet back relatively straight, surface smooth or rough; groove closed or open, margins not overlapping
 4. Stems 1–2 cm tall, < or = basal leaves; basal leaves generally < 1 cm **8. *C. roosiorum***
 - 4' Stems > 2 cm tall, > basal leaves; basal leaves generally >> 1 cm
 5. Nutlet lanceolate to lance-ovate, inner surface (between groove and margin) generally smooth, shiny **9. *C. nubigena***
 - 5' Nutlet ovate, inner surface generally rough or wrinkled
 6. Edge of nutlet groove not elevated; nutlet sculpturing finely rugose–tuberculate on dorsal and ventral surfaces **10. *C. humilis***
 - 6' Edge of nutlet groove elevated; nutlet sculpturing roughly rugose
 7. Pedicel 0.5–2 mm in fruit; calyx lobes 4.5–8 mm in fruit; trichomes on stem and leaves white **11. *C. hoffmannii***
 - 7' Pedicel 2–6 mm in fruit; calyx lobes 7–11 mm in fruit; trichomes on stem and leaves yellow to brown
 8. Biennial or short-lived perennial herbs; caudex not woody; nutlets prominently dorsally ridged or keeled **12. *C. virginensis***
 - 8' Long-lived perennial herbs; caudex woody; nutlets not prominently keeled, dorsal ridge rounded **13. *C. tumulosa***

5. *Cryptantha confertiflora* (Greene) Payson (Figure 5A–B, p.16)

Common name: Yellow-flowered cat's eye. **Distribution in Southern California:** Southwestern California region (San Bernardino Mountains), Desert mountains; Inyo, Kern, Mono, San Bernardino counties. **Conservation Status:** None. **Diagnosis:** Corolla yellow, tube exceeding calyx in length; nutlets smooth and shiny with closed ventral groove with overlapping margins.

6. *Cryptantha flavoculata* (A. Nelson) Payson (Figure 5C–D, p.16)

Common name: Yellow-eyed cat's eye. **Distribution in Southern California:** Desert mountains; Inyo, Mono, San Bernardino counties. **Conservation Status:** None. **Diagnosis:** Corolla white with prominent, bright yellow fornices, tube exceeding calyx in length; nutlets with rough sculpturing and open ventral groove with elevated margins.

7. *Cryptantha cinerea* var. *abortiva* (Greene) Cronquist (Figure 5E–H, p.16)

Common name: Bow-nut cat's eye. **Distribution in Southern California:** San Bernardino, Desert mountains; Inyo, Los Angeles, Mono, San Bernardino counties. **Conservation Status:** None. **Diagnosis:** Stems prostrate to ascending; nutlets strongly convex-curved dorsally, smooth and shiny with a closed nutlet groove. [*C. jamesii* (Torrey) Payson var. *abortiva* (Greene) Payson]

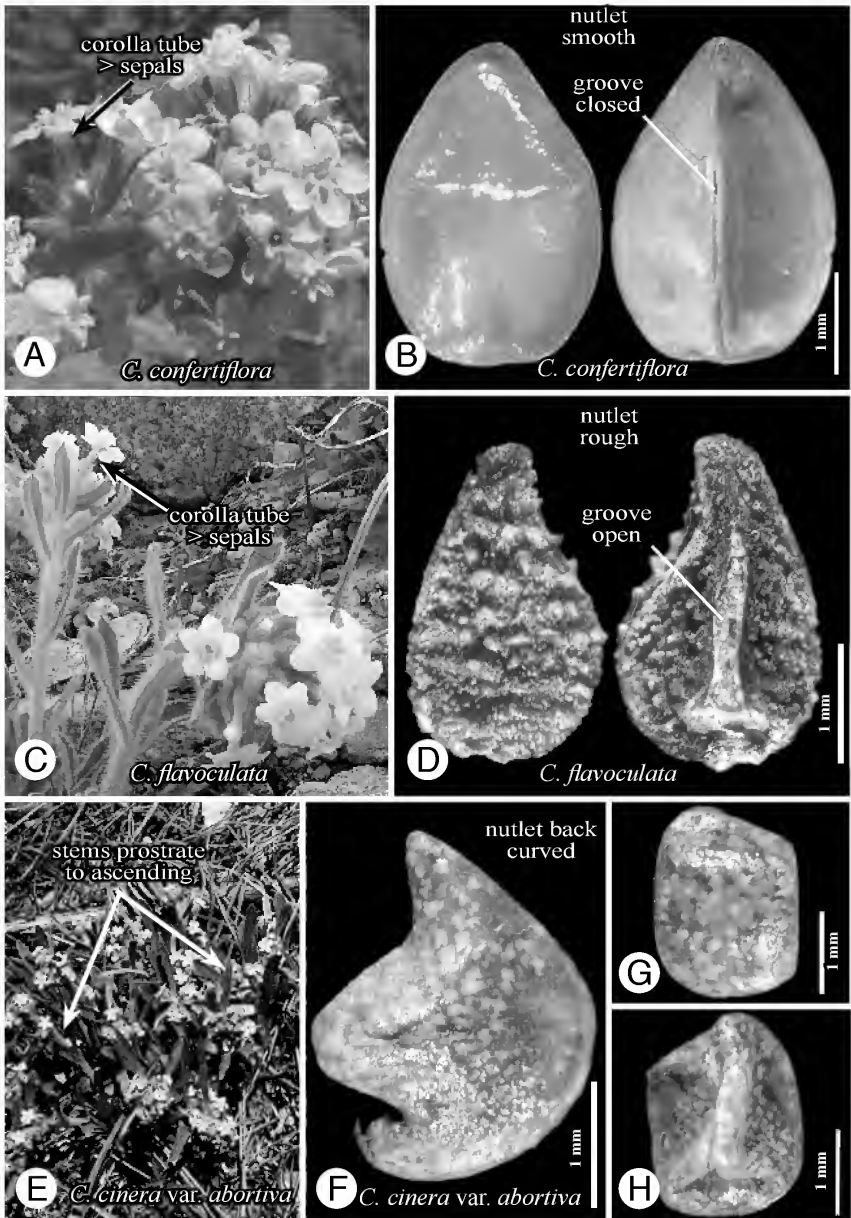


Figure 5. **A-B:** *Cryptantha confertiflora*. **A:** Inflorescence, showing corolla tube longer than calyx. **B:** Nutlet, dorsal (left) and ventral (right) views, showing smooth surface and closed groove. **C-D:** *C. flavoculata*. **C:** Inflorescence, showing long corolla tube. **D:** Nutlet, dorsal (left) and ventral (right) views, showing rough surface and open groove. **E-H:** *C. cinerea* var. *abortiva*. **E:** Plant, showing prostrate to ascending stem habit. **F:** Nutlet, side view, showing strongly curved dorsal surface. **G:** Nutlet, dorsal view. **H:** Nutlet, ventral view. Note: images at A, C, and E courtesy of Gary Monroe.

8. *Cryptantha roosiorum* Munz (Figure 6A-B, p.18)

Common name: Bristlecone cat's eye. **Distribution in Southern California:** Inyo Mountains; Inyo County. **Conservation Status:** CNPS List 1B.2. **Diagnosis:** Stems short, often equal in length with the basal leaves and generally no greater than 2 cm tall; basal leaves no greater than 1 cm long. It has a very restricted distribution in high elevation limestone soils of bristle-cone pine and limber pine forests.

9. *Cryptantha nubigena* (Greene) Payson (Figure 6C-D, p.18)

Common name: Sierra cat's eye. **Distribution in Southern California:** White and Inyo mountains, Desert mountains; Inyo, Mono, San Bernardino counties. **Conservation Status:** None. **Diagnosis:** Stems elongate, much longer than leaves; nutlets lanceolate to lance-ovate with smooth, shiny dorsal and ventral surfaces.

10. *Cryptantha humilis* (Greene) Payson (Figure 6E-F, p.18)

Common name: Low cat's eye. **Distribution in Southern California:** northern Desert mountains; Inyo, Mono counties. **Conservation Status:** None. **Diagnosis:** Stems elongate, much longer than leaves; nutlets ovate, sculpturing finely rugose on dorsal and ventral surfaces, margin of the ventral groove non-elevated.

11. *Cryptantha hoffmannii* I.M. Johnston (Figure 7A-D, p.19)

Common name: White Mountain cat's eye. **Distribution in Southern California:** White and Inyo mountains, northern Desert mountains; Inyo, Mono, San Bernardino counties. **Conservation Status:** None. **Diagnosis:** Biennial or short-lived perennial; pedicel 0.5-2mm in fruit; calyx 4.5-8 mm long; nutlet coarsely rugose, ventral groove margin elevated. It is distinguished from the closely associated species *C. virginensis* and *C. tumulosa* by the snowy-white trichomes and the smaller pedicel and fruiting calyx. It is distinguished from *C. humilis* by the coarsely rugose sculpturing on the nutlet and elevated margin of the nutlet groove. [*C. virginensis* (M.E. Jones) Payson *in part*, sensu W.A. Kelley and Wilken 1993]

12. *Cryptantha virginensis* (M.E. Jones) Payson (Figure 7E-G, p.19)

Common name: Virgin River cat's eye. **Distribution in Southern California:** White and Inyo mountains, northern and eastern Mojave Desert mountains; Inyo, Mono, San Bernardino counties. **Conservation Status:** None. **Diagnosis:** Biennial or short lived perennial; caudex slender and short-lived; pedicel 2-5 mm long in fruit; calyx 7-11 mm long; nutlet roughly rugose, dorsally carinate, ventral groove margin elevated. It differs from *C. hoffmannii* in its tawny, yellow-brown trichomes, the longer pedicel and calyx, and the dorsally carinate (keeled) nutlet.

13. *Cryptantha tumulosa* (Payson) Payson (Figure 7H-I, p.19)

Common name: New York Mountain cat's eye. **Distribution in Southern California:** eastern Mojave Desert, northern and eastern Desert mountains; Inyo, Mono, San Bernardino counties. **Conservation Status:** CNPS List 4.3. **Diagnosis:** Perennial; caudex woody; pedicel 3-6 mm long in fruit, calyx 7-10 mm long in fruit, nutlet roughly rugose, not carinate, ventral groove margin elevated. It is

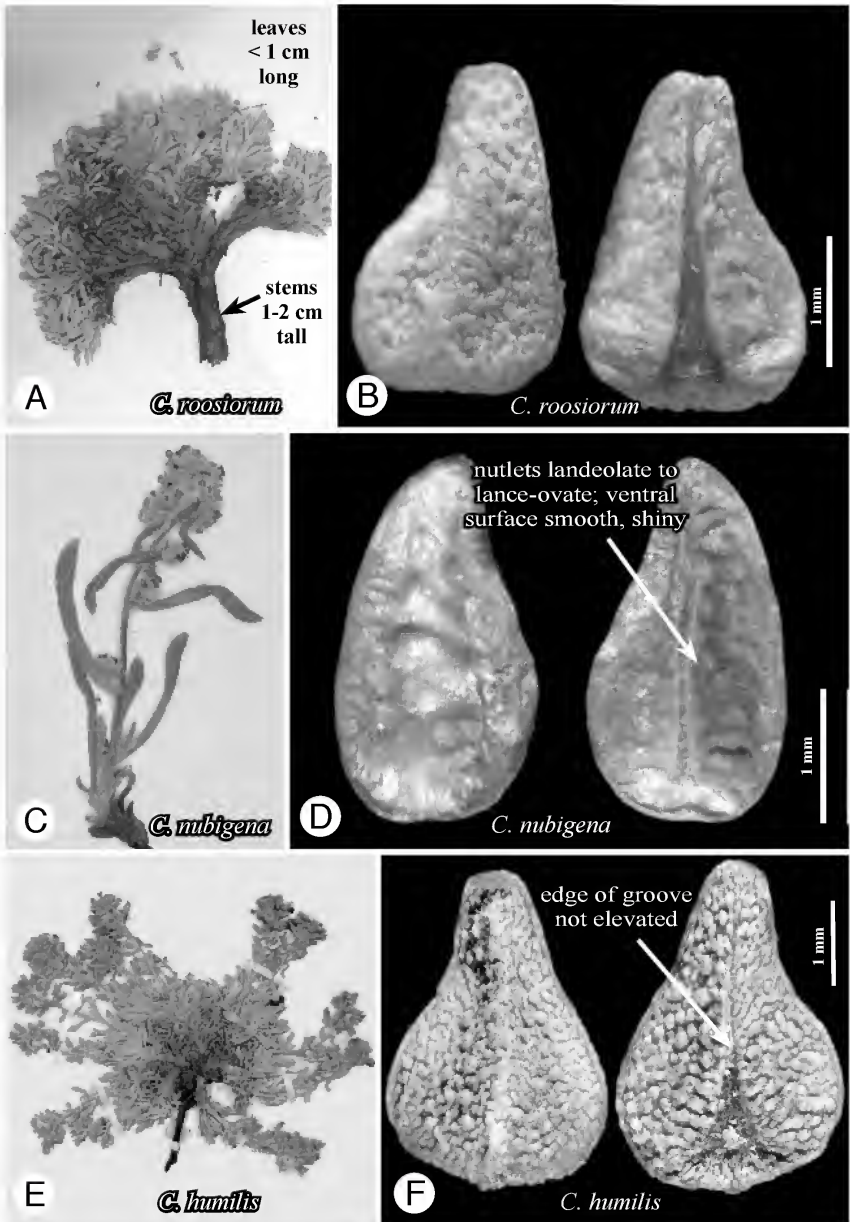


Figure 6. A-B: *Cryptantha roosiorum*. **A:** Whole plant, showing short stature and small leaves. **B:** Nutlet, dorsal (left) and ventral (right) views. **C-D: *C. nubigena*.** **C:** Whole plant. **D:** Nutlet, dorsal (left) and ventral (right) views. Note smooth, shiny ventral surface. **E-F: *C. humilis*.** **E:** Whole plant. **F:** Nutlet, dorsal (left) and ventral (right) views. Note finely rugose surface, edge of ventral groove not appreciably elevated.

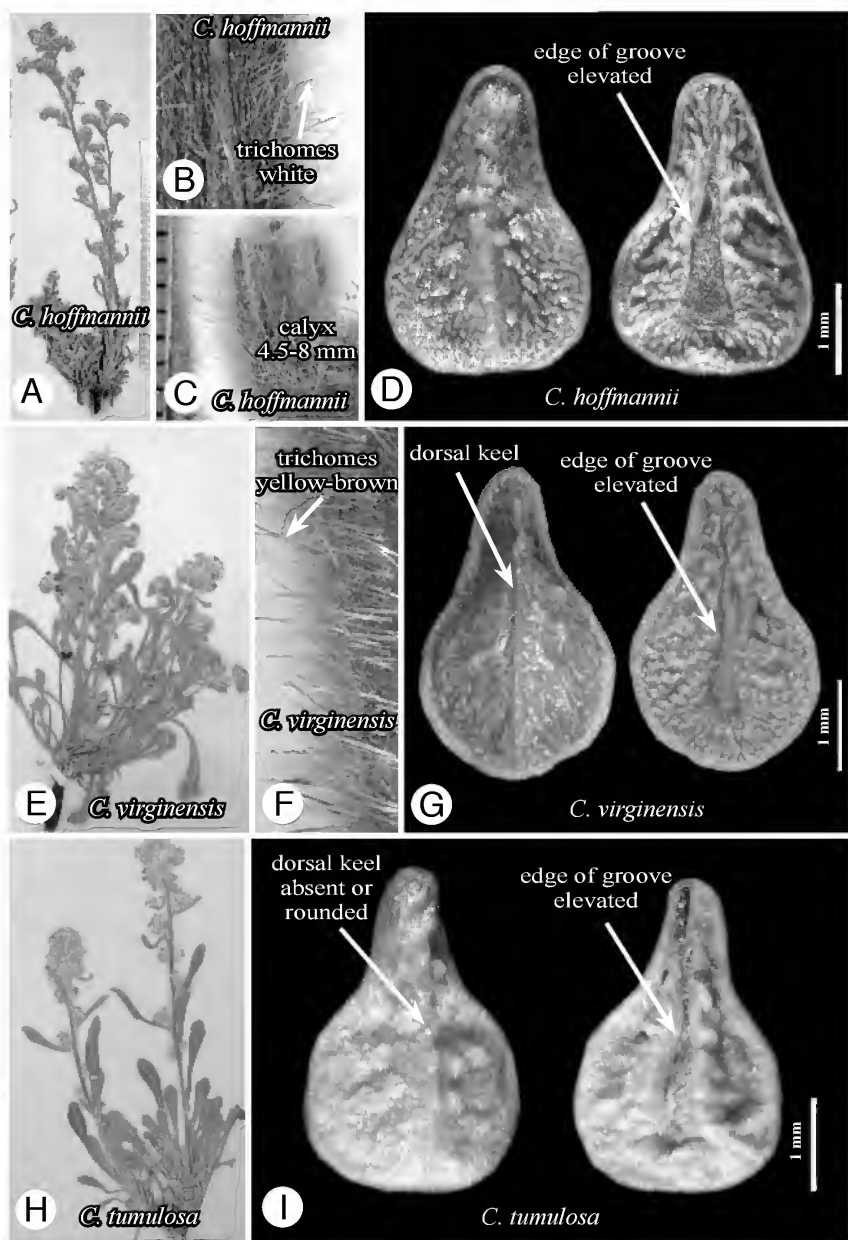


Figure 7. **A-D:** *Cryptantha hoffmannii*. **A:** Whole plant. **B:** Stem trichomes, white in color. **C:** Calyx in fruit, 4.5-8 mm long. **D:** Nutlet, dorsal (left) and ventral (right) views. Note elevated ventral groove edge. **E-G:** *C. virginensis*. **E:** Whole plant. **F:** Stem trichomes, yellow to brown in color. **G:** Nutlet, dorsal (left) and ventral (right) views. Note dorsal keel. **H-I:** *C. tumulosa*. **H:** Whole plant. **I:** Nutlet, dorsal (left) and ventral (right) views. Note absence of dorsal keel.

distinguished from closely associated *C. hoffmannii*, by its tawny, yellow-brown trichomes, and the longer (in fruit) pedicel and calyx. It differs from *C. virginensis* in having a prominently woody caudex and nutlets with a rounded dorsal ridge.

Group 4: *Krynitzkia*

The species of *Krynitzkia* (origin unknown, presumably named as a commemorative), as circumscribed by Johnston (1927) and Payson (1927), are almost certainly an unnatural, paraphyletic group (Hasenstab 2009). Almost all members are annuals (very rarely perennial) with mostly cauline leaves. The nutlets in this group are quite variable in sculpturing, number, and heteromorphism, but all have an acute to narrowly acute apex and a ventral groove that extends almost to the apex. See Figures 27, 28, 29E-H, and 30 for comparative nutlet images in the *Krynitzkia* group. For ease of identification, *Krynitzkia* is divided into two groups, based on general nutlet sculpturing.

Key to Groups of *Krynitzkia*

1. All nutlets of fruit smooth and shiny *Krynitzkia* Smooth Nutlet Group, below
- 1' At least one nutlet of fruit rough: papillate, tuberculate, and/or muricate
..... *Krynitzkia* Rough Nutlet Group, p. 29

Krynitzkia – Smooth Nutlet Group (See Figure 27 for comparative nutlet images)

[Note: an asterisk indicates that taxon also appears in the *Krynitzkia* Rough Nutlet key.]

1. Nutlet asymmetric, ventral groove off-center from nutlet body
 2. Nutlet ventral groove strongly off-center, appearing marginal; nutlets 4 per fruit; flowers in elongate inflorescence units 14. *C. affinis*
 - 2' Nutlet attachment scar edges slightly off-center, nearer one margin than the other; nutlet 1 per fruit; flowers in globose inflorescence units 15. *C. glomeriflora*
- 1' Nutlet symmetric, ventral groove central
 3. Some calyx trichomes apically hooked, sometimes basally encrusted with exudate; nutlet 1 per fruit
 4. Nutlet lance-ovate with swollen base, rounded margin, and long acuminate (caudate) apex; corolla limb 1–5(6) mm wide; calyx trichomes usually basally encrusted with exudate; common, widespread 16. *C. flaccida*
 - 4' Nutlet compressed ovate with dorsally flattened base, sharp angled margin, and ± acute apex; corolla limb 0.5–1(1.5) mm wide; calyx trichomes not basally encrusted with exudate; uncommon 17. *C. sparsiflora*
 - 3' Calyx trichomes ± straight, rarely wavy, either erect, spreading, or reflexed, not apically hooked nor basally encrusted with exudate; nutlets 1–4 per fruit
 5. Calyx sepal tips with reflexed bristles; corolla limb 0.5–1 mm wide 18. *C. nemaclada*
 - 5' Calyx sepal tips with bristles mostly spreading or ascending; corolla limb 0.5–7.5 mm wide
 6. Sepals 6–10 mm in fruit; longest sepal bristles 3–4 mm in fruit 19. *C. ganderi*
 - 6' Sepals 1–6 mm in fruit; longest sepal bristles < 3 mm in fruit
 7. Flowers gen subtended by bracts
 8. Stems gen prostrate to decumbent, greenish when in fruit; nutlets 3–4 per fruit (all smooth) 20. *C. leiocarpa*
 - 8' Stems gen erect to ascending, reddish brown when in fruit; nutlet 1 per fruit and smooth (or 2 per fruit, 1 smooth, 1 rough) * 21. *C. maritima*

- 7' Flower bracts absent
 - 9. Calyx obconic at base; calyx trichomes dense, straight, ascending, relatively soft, sepal midvein hairs slightly longer, but not bristly **22. *C. gracilis***
 - 9' Calyx rounded at base, with both appressed, soft trichomes and ascending to spreading, stiff, bristle-like trichomes
 - 10. Sepals ≤ 1 mm in fl, 1–2 mm in fruit **23. *C. microstachys***
 - 10' Sepals > 1 mm in fl, ≥ 3 mm in fruit
 - 11. Nutlets 1–1.5 mm long, 1–4 per fruit ***C. clevelandii***
 - 12. Pedicels 0–0.5 mm, becoming erect, \pm appressed to stem in fruit; calyx (2.5)3–3.5 mm in fruit, narrow at base, sepals linear in fruit; corolla limb 1–2.5 mm wide; corolla fornicies pale yellow; nutlets 1–2 per fruit **24. *C. clevelandii* var. *clevelandii***
 - 12' Pedicels 0.5–1 mm, \pm inclined, not appressed to stem in fruit; calyx 3–4(4.5) mm in fruit, \pm wide at base, sepals ovate in fruit; corolla limb (2)2.5–5 mm wide; corolla fornicies yellow; nutlets 3–4(1) per fruit **25. *C. clevelandii* var. *florosa***
 - 11' Nutlets 1.5–2 mm long, 4 per fruit
 - 13. Nutlet margin gen rounded throughout, sometimes angled below middle **26. *C. torreyana***
 - 13' Nutlet margin angled (obtuse in cross-section), esp near tip
 - 14. Corolla limb (4)5–7.5 mm wide; nutlets ovate to lance-ovate **27. *C. mohavensis***
 - 14' Corolla limb 2–3 mm wide; nutlets lanceolate to lance-ovate **28. *C. watsonii***
- 14. *Cryptantha affinis* (A. Gray) Greene** (Figure 8A, p.22)
Common name: Side-grooved cryptantha. **Distribution in Southern California:** Southwestern California region (Transverse and Peninsular Ranges); Kern, Los Angeles, Mono, San Bernardino, San Diego, and Ventura counties. **Conservation Status:** None. **Diagnosis:** Nutlets 4 per fruit with a very eccentric ventral groove appearing to be marginal; inflorescences with straight clusters of flowers.
- 15. *Cryptantha glomeriflora* Greene** (Figure 8B,C, p.22)
Common name: Trukee cryptantha. **Distribution in Southern California:** White mountains; Mono County. **Conservation Status:** CNPS List 4.3. **Diagnosis:** Nutlet 1 per fruit with a slightly off-center ventral groove; inflorescence with globose clusters of flowers.
- 16. *Cryptantha flaccida* (Lehmann) Greene** (Figure 8D-E, p.22)
Common name: Weak-stemmed cryptantha. **Distribution in Southern California:** Southwestern California region (western Transverse Ranges, eastern San Bernardino mountains, South Coast, Peninsular Ranges), Tehachapi mountains; Inyo, Kern, Los Angeles, Riverside, Santa Barbara, San Diego, Ventura counties. **Conservation Status:** none. **Diagnosis:** Calyx apically hooked, trichomes usually basally encrusted with exudate; nutlet 1 per fruit, lance-ovoid with a swollen base, rounded margin, and long acuminate apex.

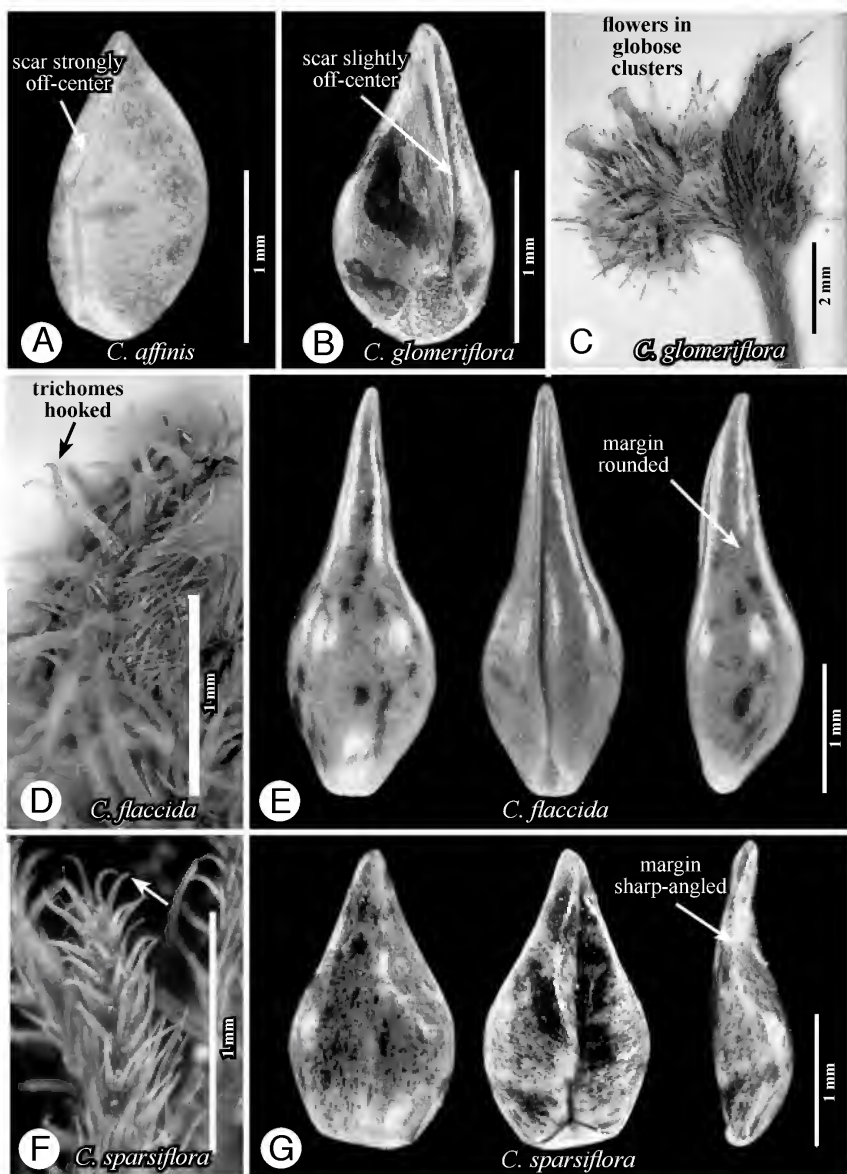


Figure 8. **A:** *Cryptantha affinis*, nutlet, ventral view, showing strongly off-center ventral groove. **B-C:** *C. glomeriflora*. **B:** Nutlet, ventral view, showing slightly off-center (asymmetric) ventral groove. **C:** Inflorescence unit, a tightly clustered, globose circinate cyme. **D-E:** *C. flaccida*. **D:** Sepal, showing hooked (uncinate) trichomes (arrow). **E:** Nutlet, dorsal, ventral, and lateral views (left to right). Note lanceolate shape, globose base, rounded margin, and elongate, acuminate (caudate) apex. **F-G:** *C. sparsiflora*. **F:** Sepal, showing hooked (uncinate) trichomes (arrow). **G:** Nutlet, dorsal, ventral, and lateral views (left to right). Note ovate shape, dorsally flattened base, sharp-angled margin, and short, acute apex.

17. *Cryptantha sparsiflora* (Greene) Greene (Figure 8F-G, p.22)
Common name: Few-flowered cryptantha. **Distribution in Southern California:** Southwestern California region (South Coast), Tehachapi mountains; Kern, Ventura counties. **Conservation Status:** none. **Diagnosis:** Calyx trichomes apically hooked, not basally encrusted with exudate; nutlet 1 per fruit, ovate with dorsally flattened base, sharp-angled margin, and acute apex. [*C. flaccida* (Lehmann) Greene *in part*, sensu W.A. Kelley and Wilken 1993]

18. *Cryptantha nemaclada* Greene (Figure 9A-B, p.24)
Common name: Colusa cryptantha. **Distribution in Southern California:** Southwestern California region (western Transverse Ranges), Tehachapi mountains; Kern, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Sepal apices with reflexed trichomes; nutlets 1-2 (4) per fruit.

19. *Cryptantha ganderi* I.M. Johnst. (Figure 9C-D, p.24)
Common name: Gander's cryptantha. **Distribution in Southern California:** western Sonoran Desert; San Diego County (Borrego Valley). **Conservation Status:** CNPS List 1B.1. **Diagnosis:** Sepals relatively long (6-10 mm) with long (3-4 mm) sepal bristles; nutlets large (2-2.5 mm long).

20. *Cryptantha leiocarpa* (Fisher & C. A. Meyer) Greene (Figure 9E, 9G, p.24)
Common name: Beach cryptantha. **Distribution in Southern California:** Southwestern California region (northern South Coast); Los Angeles, Orange, Santa Barbara, and Ventura counties. **Conservation Status:** none. **Diagnosis:** Plant decumbent; stems greenish at maturity; flowers bracteate; nutlet 1 per fruit.

21. *Cryptantha maritima* (Greene) Greene var. *maritima* (Figure 9F, 9H, 19A-C, p.24, 40)
Common name: Maritime cryptantha. **Distribution in Southern California:** Southwestern California region (South Coast, Channel Islands, Transverse Ranges, Peninsular Ranges), Desert province; Imperial, Inyo, Los Angeles, Riverside, Santa Barbara, San Bernardino, San Diego, and Ventura counties. **Conservation Status:** none. **Diagnosis:** Plants erect; stems reddish at maturity; flowers bracteate; nutlets either 1 per fruit and smooth or 2 per fruit with one smooth and one tuberculate. [*C. maritima* var. *pilosa* I.M. Johnston is purported to differ from *C. maritima* var. *m.* in having dense tufts of soft (pilose) trichomes arising from the calyx, but this feature forms a grade is not diagnostic, sensu R.A. Kelly (*in prep*); *C. maritima* var. *cedrocensis* (Greene) I.M. Johnston, endemic to Cedros Island, Baja California, Mexico, differs in having 4 nutlets (Wiggins 1980)]

22. *Cryptantha gracilis* Osterh. (Figure 10A-B, p.26)
Common name: Slender cryptantha. **Distribution in Southern California:** Desert province (eastern Mojave Desert and mountains), White and Inyo mountains; Inyo, Mono, San Bernardino counties. **Conservation Status:** none. **Diagnosis:** Calyx obconical, with ascending, soft trichomes; nutlet 1 (2,3) per fruit, 3-sided.

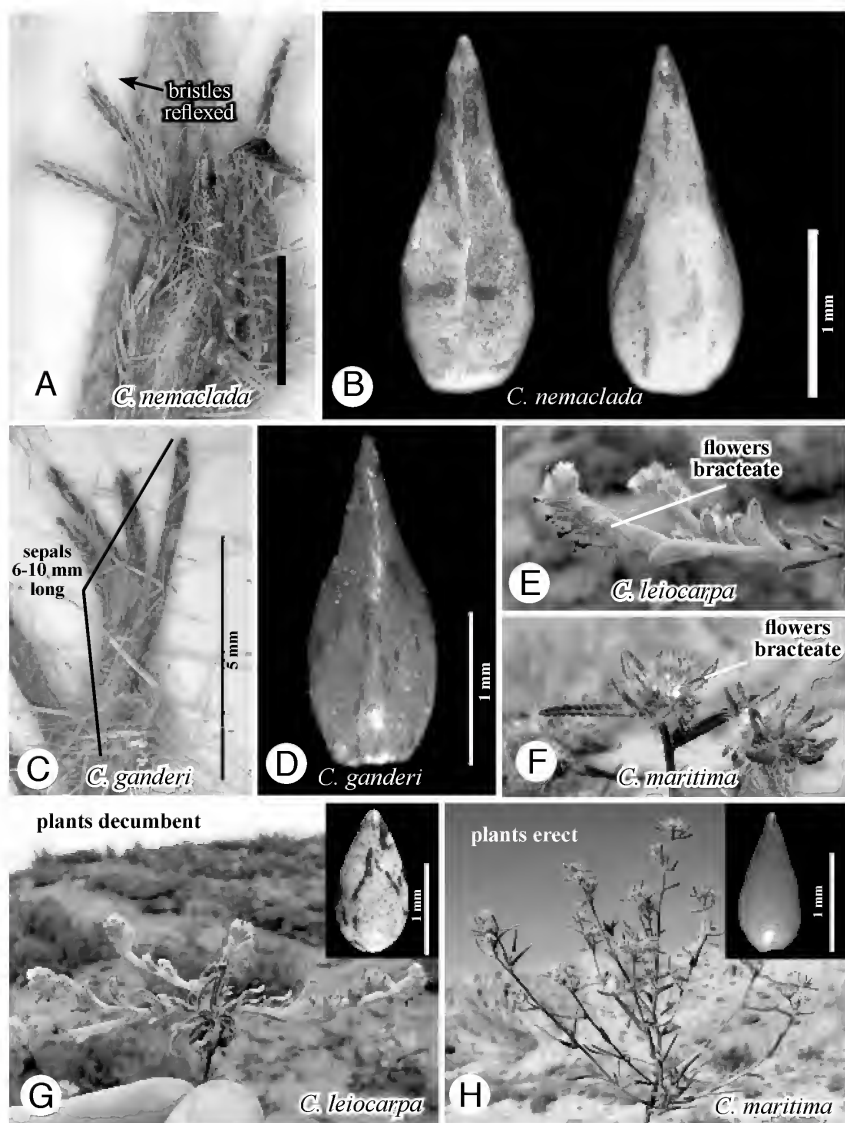


Figure 9. **A-B:** *Cryptantha nemaclada*. **A:** Calyx, showing short, reflexed bristles near apex. **B:** Nutlet, ventral (left) and dorsal (right) views. **C-D:** *C. ganderi*. **C:** Calyx. Note long length. **D:** Nutlet, dorsal view. **E&G:** *C. leiocarpa*. **E:** Inflorescence branch, showing bracteate flowers. **G:** Plant from field, showing decumbent branching. Inset: Nutlet, dorsal view. **F&H:** *C. maritima*. **F:** Inflorescence, showing bracteate flowers. **H:** Plant, showing erect to ascending branches. Inset: Nutlet, dorsal view.

23. *Cryptantha microstachys* (A. Gray) Greene (Figure 10C-E, p.26)

Common name: Tejon cryptantha. **Distribution in Southern California:** Southwestern California region (Transverse Ranges, Peninsular Ranges, South Coast, Santa Catalina Island); Kern, Los Angeles, Orange, Riverside, Santa Barbara, San Bernardino, San Diego, and Ventura counties. **Conservation Status:** none. **Diagnosis:** Calyx small, short (≤ 1 mm in fl, 1–2 mm in fr); nutlet usually solitary.

24. *Cryptantha clevelandii* Greene var. *clevelandii* (Figure 10F-H, p.26)

Common name: Cleveland's cryptantha. **Distribution in Southern California:** Southwestern California region (South Coast); Los Angeles, Santa Barbara, San Diego counties. **Conservation Status:** none. **Diagnosis:** Flowers ebracteate; pedicels absent to short (0–0.5 mm), becoming appressed to the stem in fruit; calyx basally narrowed with straight, non-reflexed, soft and bristle-like trichomes, the calyx (2.5)3–3.5 mm in fruit; corolla 1–2.5 mm wide; nutlets 1–2 per fruit (1–1.5 mm long).

25. *Cryptantha clevelandii* Greene var. *florosa* I.M. Johnst. (Figure 11A-D, p.27)

Common name: Coastal cryptantha. **Distribution in Southern California:** Southwestern California region (South Coast, Channel Islands); Kern, Los Angeles, Orange, Riverside, Santa Barbara, San Bernardino, San Diego, and Ventura counties. **Conservation Status:** none. **Diagnosis:** This variety differs in having longer (0.5–1 mm) pedicels that become inclined (not appressed) to the stem in fruit, a longer (3–4 mm long), basally wide calyx (in fruit), a wider (2.5–5 mm) corolla limb, and nutlets 3–4(1) per fruit. [*C. clevelandii* Greene *in part*, sensu W.A. Kelley and Wilken 1993]

26. *Cryptantha torreyana* (A. Gray) Greene (Figure 11E-J, p.27)

Common name: Torrey's cryptantha. **Distribution in Southern California:** Southwestern California region (western Transverse Ranges), White mountains; Inyo, Kern, and Ventura counties. **Conservation Status:** none. **Diagnosis:** Flowers ebracteate; calyx with a rounded base and straight, non-reflexed trichomes; nutlets symmetrical (1.5–2 mm long), 4 per fruit, with rounded margins.

27. *Cryptantha mohavensis* (Greene) Greene (Figure 12A-B, p.28)

Common name: Mohave cryptantha. **Distribution in Southern California:** Tehachapi mountains, western Mohave Desert, edge of desert only, mostly found along the desert slope of mountains; Inyo, Kern, Los Angeles, San Bernardino counties. **Conservation Status:** none. **Diagnosis:** Flowers ebracteate; calyx with a rounded base (1–6 mm long), trichomes straight, non-reflexed; corolla limb relatively large (4–7.5 mm wide); nutlets symmetrical, ovate to lance-ovate (ca. 2 mm long), 4 per fruit, with distinctly angled margins.

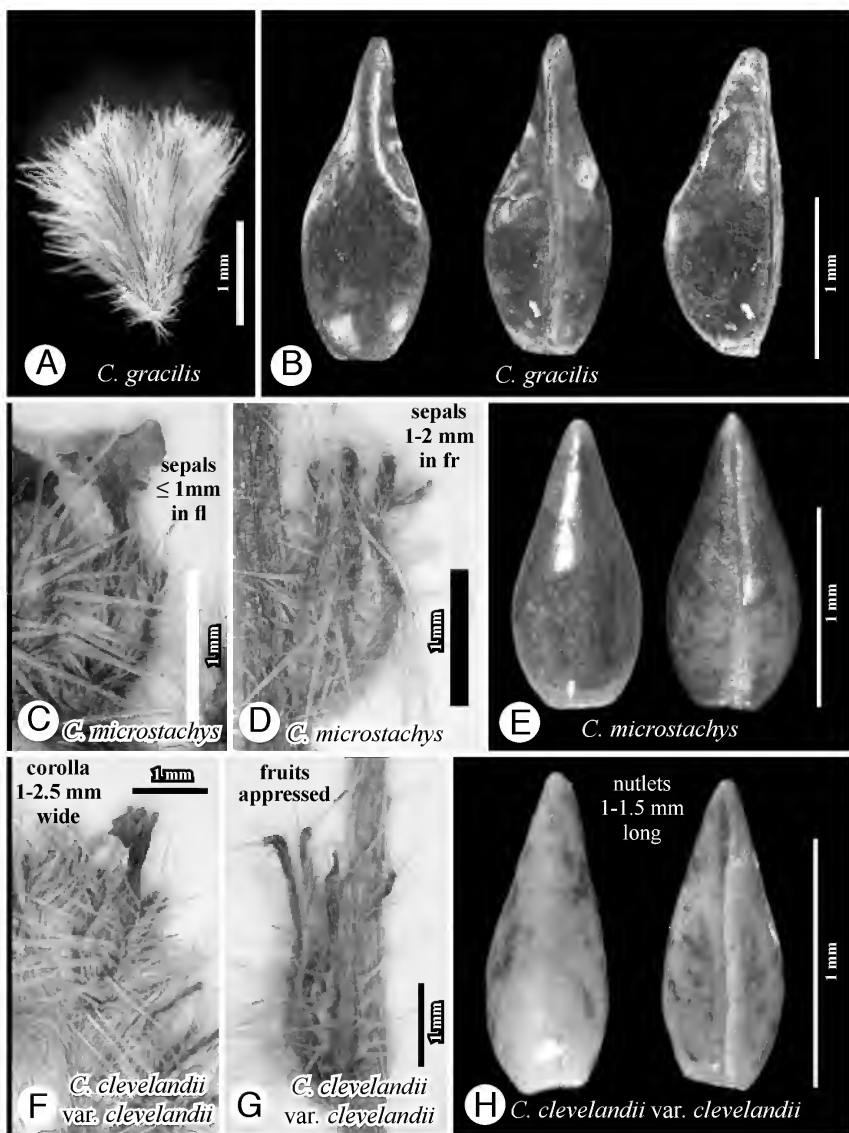


Figure 10. **A-B:** *Cryptantha gracilis*. **A:** Calyx, showing characteristic obconic base and long, soft trichomes. **B:** Nutlet, dorsal, ventral, and lateral views (left to right). **C-E:** *C. microstachys*. **C:** Flower. Note short calyx. **D:** Fruit, also with short calyx. **E:** Nutlet, dorsal (left) and ventral (right) views. **F-H:** *C. clelandii* var. *clelandii*. **F:** Flower, showing small corolla. **G:** Fruit. Note appressed orientation. **H:** Nutlet, dorsal (left) and ventral (right) views.

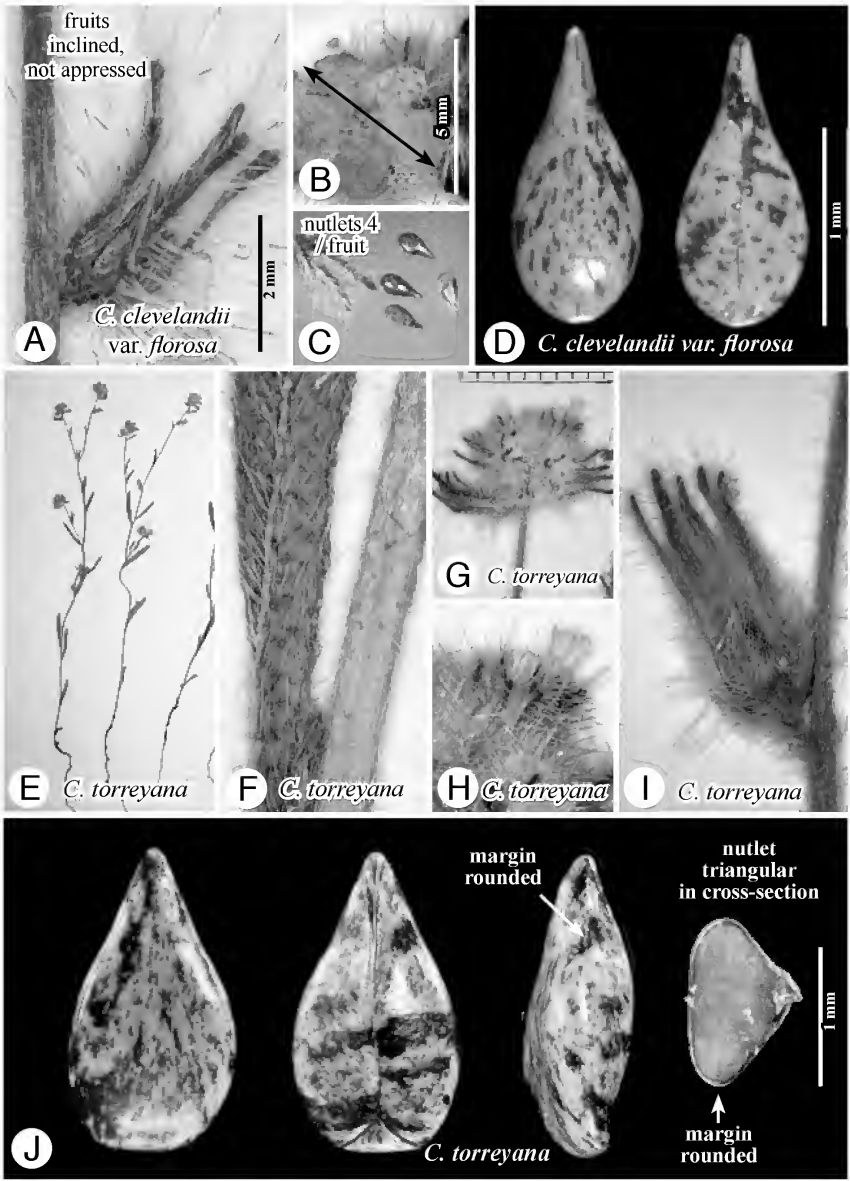


Figure 11. A-D: *Cryptantha clelandii* var. *florosa*. **A:** Fruit, showing inclined orientation. **B:** Corolla, relatively wide in size. **C:** Fruit, showing 4 nutlets. **D:** Nutlet, dorsal (left) and ventral (right) views. **E-J: *C. torreyana*.** **E:** Whole plants from herbarium specimen. **F:** Close-up of leaf (left) and stem (right). **G:** Young inflorescence. **H:** Flower. **I:** Fruit. **J:** Nutlet, dorsal, ventral, lateral, and cross-sectional views (left to right). Note triangular shape and rounded margins.

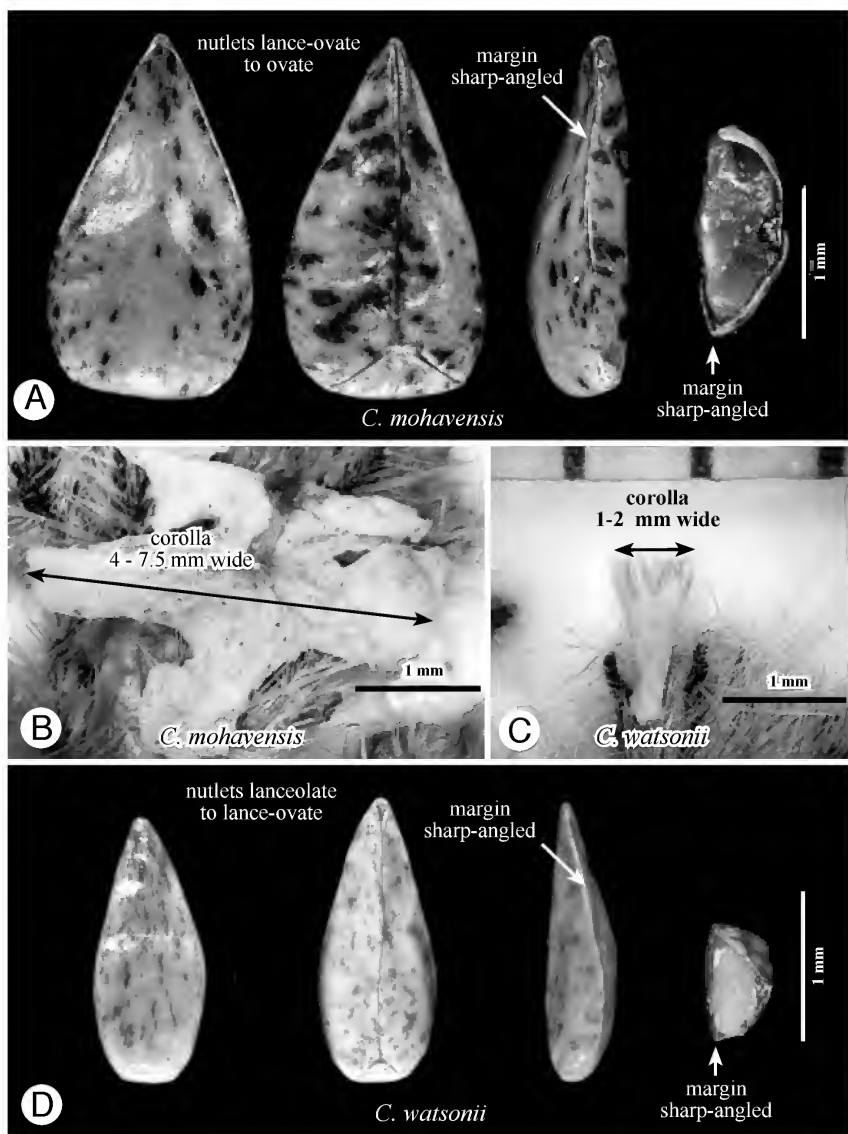


Figure 12. A-B: *Cryptantha mohavensis*. **A:** Nutlet, dorsal, ventral, lateral, and cross-sectional views (left to right). Note ovate shape and rounded ventral face (far right) and sharp-angled margins. **B:** Corolla, with wide limb. **C-D: *C. watsonii*.** **C:** Corolla, with short limb. **D:** Nutlet, dorsal, ventral, lateral, and cross-sectional views (left to right). Note lanceolate shape and sharp-angled margins.

28. *Cryptantha watsonii* (A. Gray) Greene (Figure 12C-D, p.28)

Common name: Watson's cryptantha. **Distribution in Southern California:** White and Inyo mountains; Inyo, Mono counties. **Conservation Status:** none. **Diagnosis:** Flowers ebracteate; calyx with a rounded base (1-6 mm long), trichomes straight, non-reflexed; corolla relatively small (limb 1-2 mm wide); nutlets lanceolate to lance-ovate (1.5-2 mm long), 4 per fruit, with distinctly angled margins.

***Krynitzkia* – Rough Nutlet Group** (See Figure 28, 29E-H, 30 for nutlet images)

[Note: an asterisk indicates that taxon appears in the *Krynitzkia* Smooth Nutlet key or in more than 1 couplet.]

1. One or more nutlets of fruit with margin sharp-angled and flattened as a narrow rim or a narrow to broad wing
 2. Pedicels 1–4 mm long in fruit; plant annual or perennial
 3. Nutlets homomorphic, dorsally tuberculate-papillate, margin with narrow, flattened rim or wing; plant usu. annual, with major central axis; inflorescence in fruit dense **29. *C. holoptera***
 - 3' Nutlets heteromorphic, 1 longer and dorsally papillate to papillate-tuberculate, 2–3 shorter and dorsally papillate-tuberculate, margins with very narrow, flattened rim; plant perennial (but may flower first year), without major, central axis; inflorescence in fruit open **30. *C. racemosa***
 - 2' Pedicels 0–1 mm long in fruit; plant annual
 4. Nutlet 1 (rarely 2) per fruit; fruit sepals ovate-elliptic, nutlet margin sharp-angled to rimmed, dorsal tubercles minutely spinulose **31. *C. utahensis***
 - 4' Nutlets usu. 4 per fruit; fruit sepals linear-lanceolate, nutlet margin winged along entire margin, dorsal tubercles, if present, not spinulose
 5. At least some nutlets with prominent, strongly lobed wings ***C. pterocarya***
 6. Nutlets heteromorphic, 3 nutlets winged, 1 not winged
 7. Wing of winged nutlets very broad **32. *C. p. var. pterocarya***
 - 7' Wing of winged nutlets narrow, knifelike **33. *C. p. var. purpusii***
 - 6' Nutlets homomorphic, all 4 nutlets with prominent wings **34. *C. p. var. cycloptera***
 - 5' Nutlets sharp-angled, rimmed, or narrowly winged (not strongly lobed)
 8. Nutlets homomorphic
 9. Corolla limb 4–9 mm wide; calyx in fruit 3–4 mm long; nutlets 2–2.5 mm long, narrowly winged (wings sometimes toothed), dorsal surface coarsely tuberculate; flowers ebracteate **35. *C. oxygona***
 - 9' Corolla limb 1–3 mm wide; calyx in fruit 4–6 mm long; nutlets 1.5–2 mm long, narrowly winged (wings sharp, never toothed), dorsal surface finely tuberculate; flowers bracteate (bracts deciduous) **36. *C. costata***
 - 8' Nutlets heteromorphic by size, one distinctly larger than the other three
 10. Nutlet margin rimmed and knife-like to narrowly winged; small nutlets ca. 1.3 mm long **37. *C. inaequata***
 - 10' Nutlet margin sharp-angled to slightly rimmed (usually rounded); small nutlets ca. 1 mm long *** 38. *C. angustifolia***
 - 1' All nutlets of fruit with margin rounded, ridged, or sharp-angled (acute to obtuse), but not flattened as a rim or wing
 11. Nutlets 2-4 per fruit, heteromorphic by size, one nutlet larger than the other(s)
 12. Nutlets 4 per fruit, similar in sculpturing
 13. Plants erect; nutlets lance-ovate, small nutlets ca. 1 mm long, finely papillate, ventral groove narrow *** 38. *C. angustifolia***

- 13' Plants sprawling; nutlets narrowly lanceolate, small nutlets ca. 2 mm long, tuberculate-papillate, ventral groove wide 39. *C. dumetorum*
- 12' Nutlets 2–4 per fruit, different in sculpturing, the larger nutlet smooth to mostly smooth, the smaller nutlet(s) papillate to tuberculate
14. Nutlets 4 per fr, < 1 mm long, triangular–ovate; flower bracts absent; calyx in fruit sub–globose with hooked trichomes, sepals 1–1.5 mm long 40. *C. micromeres*
- 14' Nutlets 2 per fruit, 1.5–2 mm long, oblong–lanceolate; flower bracts present, calyx in fruit oblong with straight trichomes, sepals 2–3 mm long * 21. *C. maritima*
- 11' Nutlets 1–4 per fruit, homomorphic in size and sculpturing
15. Nutlets lanceolate (length:width ratio $\geq 3:1$)
16. Nutlet 1 (–2) per fruit
17. Mature fruit strongly recurved from stem; nutlet incurved 41. *C. recurvata*
- 17' Mature fruit not recurved from stem; nutlet(s) not incurved
18. Corolla limb 1–1.5 mm wide, deserts 42. *C. decipiens*
- 18' Corolla limb 3–5 mm wide, cismontane 43. *C. corollata*
- 16' Nutlets usu. 4 per fruit
19. Calyx 6–10 mm long; nutlets coarsely tuberculate *C. nevadensis*
20. Plants 20–60 cm tall; secondary branches sprawling; sepals strongly recurved at tips; corolla limb 1–2 mm wide 44. *C. nevadensis* var. *nevadensis*
- 20' Plants <20 cm tall; secondary branches ascending; sepals erect to slightly recurved at tips; corolla limb 2–4 (5) mm wide 45. *C. nevadensis* var. *rigida*
- 19' Calyx 4–6 mm long; nutlets finely tuberculate–spinulose 46. *C. scoparia*
- 15' Nutlets lance–ovate, ovate, or triangular–ovate (length:width ratio < 3:1)
21. Nutlet dorsal surface with at least a faint median ridge *C. muricata*
22. Corolla limb 1–2.5 mm wide; nutlets brownish
23. Stem bearing, from top to below middle, many short, flower–bearing branchlets from a larger, primary axis, forming an elongate, leafy, thyrses inflorescence 47. *C. muricata* var. *jonesii*
- 23' Stem loosely and sparsely branched, without a larger primary axis 48. *C. muricata* var. *denticulata*
- 22' Corolla limb 3–8 mm wide, nutlets grayish 49. *C. muricata* var. *muricata*
- 21' Nutlet dorsal surface lacking median ridge
24. Corolla limb 3–9 mm wide
25. Sepals 2–3 mm in flower, 3.5–5 mm in fruit 50. *C. intermedia* var. *intermedia*
- 25' Sepals 4–6 mm in flower, 5–10 mm in fruit 51. *C. barbigera* var. *fergusoniae*
- 24' Corolla limb 1–2 mm wide
26. Nutlets 1–1.5 (1.8) mm long; flowers bracteate; southern Channel Islands 52. *C. traskiae*
- 26' Nutlets 1.5–3 mm long; flowers ebracteate; mainland
27. Nutlet dorsal face flattened to low–convex, densely papillate, sparsely tuberculate 53. *C. simulans*
- 27' Nutlet dorsal face convex, densely tuberculate, papillate or not
28. Nutlets ca. 3 mm long, turbercle tips translucent 54. *C. clokeyi*
- 28' Nutlets 1.5–2 mm long, turbercle tips not translucent
29. Calyx in fruit 5–6 mm long; nutlets gen 4, ovate, sculpturing finely tuberculate and papillate; corolla limb 1–1.5 mm wide 55. *C. echinella*
- 29' Calyx in fruit 5–10 mm long; nutlets 1–4, lanceolate to ovate, sculpturing coarsely tuberculate to muricate, not papillate; corolla limb 1–2.5 mm wide 56. *C. barbigera* var. *barbigera*

29. *Cryptantha holoptera* (A. Gray) J.F. Macbr. (Figure 13A-C, p.32)

Common name: Winged cryptantha. **Distribution in Southern California:** eastern Mohave Desert, Sonoran Desert; Imperial, Inyo, Los Angeles, Riverside, San Bernardino, and San Diego counties. **Conservation Status:** CNPS List 4.3. **Diagnosis:** Annual duration (sometimes perennial); stems with a major axis (inflorescence “dense”); pedicels long (1-4 mm); nutlets homomorphic, tuberculate-papillate, narrowly winged (4 per fruit).

30. *Cryptantha racemosa* (S. Watson) Greene (Figure 13D-G, p.32)

Common name: Bushy cryptantha. **Distribution in Southern California:** Southwestern California region (northern San Bernardino mountains, eastern Peninsular Ranges), Desert province, northern White and Inyo mountains; Imperial, Inyo, Los Angeles, Mono, Riverside, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Perennial duration; stems without a single, major axis (inflorescence “open”); pedicels long (1-4 mm); nutlets heteromorphic, papillate to tuberculate-papillate, narrowly winged (4 per fruit).

31. *Cryptantha utahensis* (A. Gray) Greene (Figure 14A-D, p.33)

Common name: Utah/scented cryptantha. **Distribution in Southern California:** Desert province, White and Inyo mountains; Inyo, Kern, Los Angeles, Riverside, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Pedicels short (<1 mm); nutlet 1 per fruit, with distinctive tuberculate-spinulose processes and a sharp-angled to rimmed margin.

32. *Cryptantha pterocarya* (Torrey) Greene var. *pterocarya*

(Figure 14E-G, 15A-B, p.33, 34)

Common name: Fringe nut cryptantha. **Distribution in Southern California:** Southwestern California region (eastern Peninsular Ranges), Desert province, White and Inyo mountains, often found in rocky uplands; Imperial, Inyo, Kern, Los Angeles, Mono, Riverside, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Pedicels short (<1 mm); nutlets 4 per fruit, at least some of which have distinctive, strongly lobed wings. This variety is distinguished from the other two by the heteromorphic nutlets, three of which have broad (>0.5 mm), strongly lobed wings and one of which is unwinged.

33. *Cryptantha pterocarya* (Torrey) Greene var. *purpusii* Jeps. (Figure 15D-E, p.34)

Common name: Argus Mountains cryptantha. **Distribution in Southern California:** Southwestern California region (Peninsular Ranges, Transverse Ranges), Desert province, White and Inyo mountains; Imperial, Inyo, Kern, Los Angeles, Riverside, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Pedicels short (<1 mm); nutlets 4 per fruit, at least some of which have distinctive, strongly lobed wings. This variety is distinguished from the other two in having heteromorphic nutlets, three of which have narrow (<0.5 mm), lobed wings and one of which is unwinged. [*C. pterocarya* (Torrey) Greene *in part*, sensu W.A. Kelley and Wilken 1993]

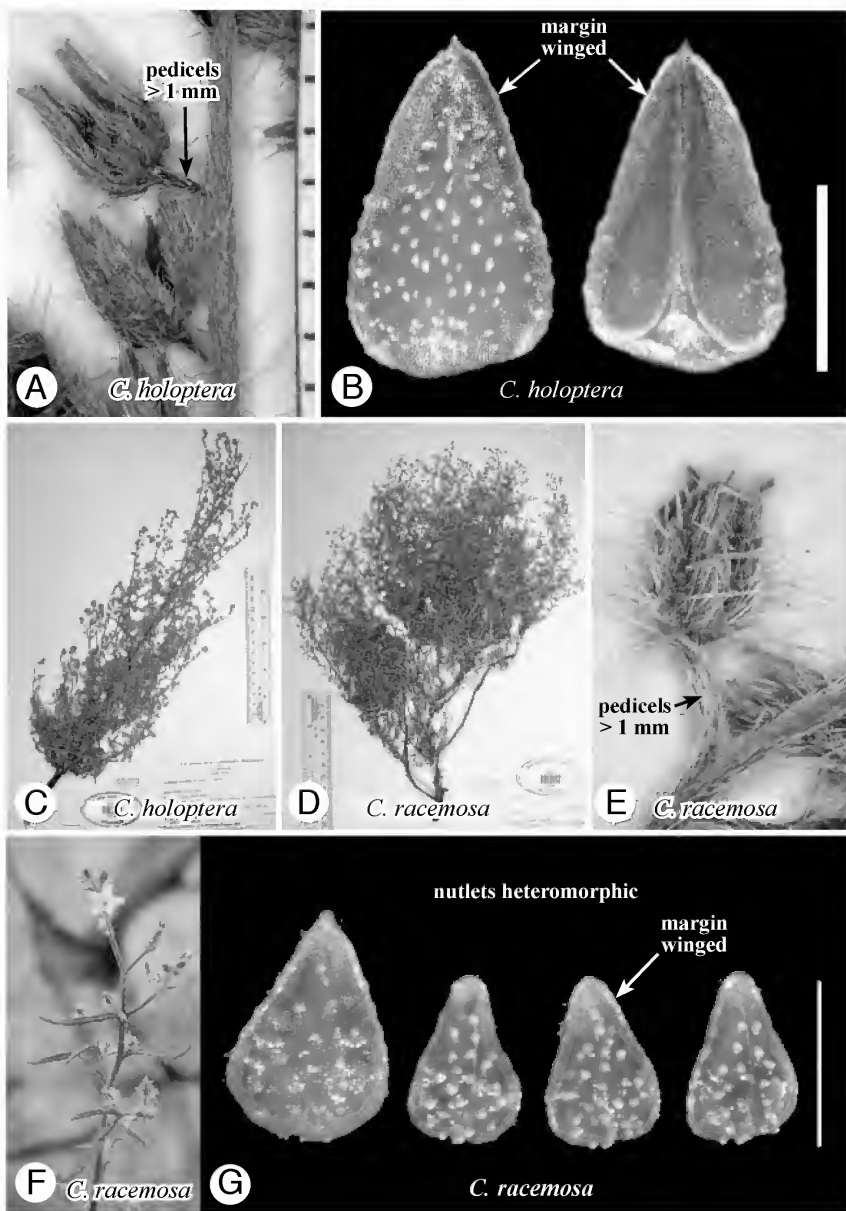


Figure 13. A-C: *Cryptantha holoptera*. **A:** Fruit, showing relatively long pedicel. **B:** Nutlet, dorsal (left) and ventral (right) views. Note ovate-triangular shape, narrow winge and scattered tubercles. **C:** Whole plants, showing single, major axis. **D-G: *C. racemosa*.** **D:** Whole plants, showing dense banching with no major primary axis. **E:** Fruit, showing long pedicel. **F:** Inflorescence. **G:** Nutlets from a single fruit, dorsal view. Note size heteromorphism.

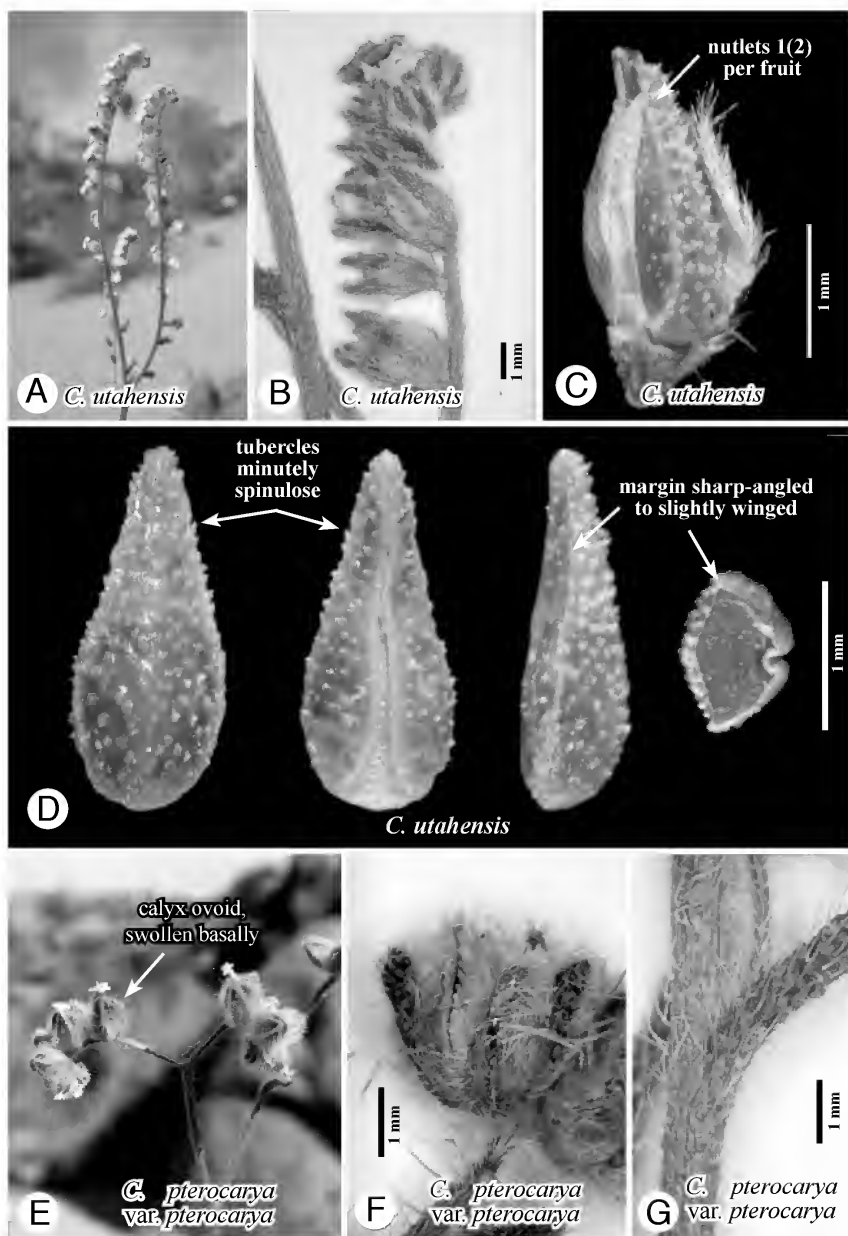


Figure 14. A-D: *Cryptantha utahensis*. **A:** Mature, elongate inflorescence. **B:** Inflorescence unit. Note narrowly elliptic sepals. **C:** Fruit, showing single nutlet. **D:** Nutlet, dorsal, ventral, lateral, and cross-sectional views (left to right). Note sharp-angled ridge and spinulose sculpturing. **E-G: *C. pterocarya* var. *pterocarya*.** **E:** Inflorescence, showing swollen, ovoid calyx and small corollas. **F:** Mature fruit, with four nutlets. **G:** Close-up of stem (below and right) and leaf (upper left).

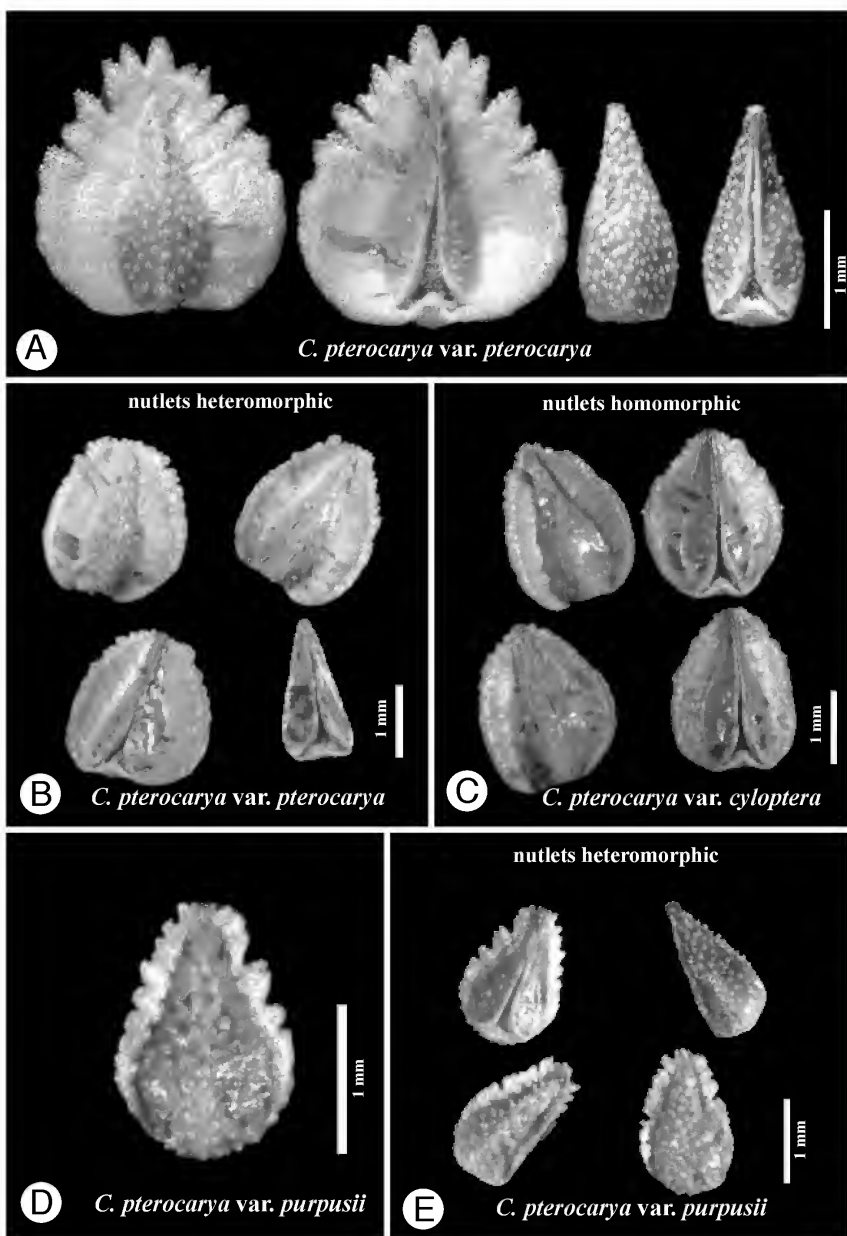


Figure 15. A-B: *Cryptantha pterocarya* var. *pterocarya*. **A:** Heteromorphic nutlets of same fruit. Left: one of three winged nutlets (dorsal and ventral views). Right: Single unwinged nutlet, dorsal and ventral views. **B:** Nutlets of a common fruit, heteromorphic: three winged, one unwinged. **C: *C. pterocarya* var. *cycloptera*.** Nutlets homomorphic, all winged. **D-E: *C. pterocarya* var. *purpusii*.** **D:** Nutlet, dorsal view. Note narrow, lobed wing. **E:** Nutlets of a common fruit, heteromorphic: three winged, one unwinged.

34. *Cryptantha pterocarya* (Torrey) Greene var. *cycloptera* (Greene) J.F. Macbr. (Figure 15C, p.34)

Common name: Tucson cryptantha. **Distribution in Southern California:** Southwestern California region (eastern Peninsular Ranges), Desert province, White and Inyo mountains, lower elevations of the desert; Imperial, Inyo, Riverside, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Pedicels short (<1 mm); nutlets 4 per fruit, at least some of which have distinctive, strongly lobed wings. This variety is distinguished from the other two in having homomorphic nutlets, all of which have broad (>0.5 mm), strongly lobed wings. [*C. pterocarya* (Torrey) Greene *in part*, sensu W.A. Kelley and Wilken 1993]

35. *Cryptantha oxygona* (A. Gray) Greene (Figure 16A-E, p.36)

Common name: Sharp nut cryptantha. **Distribution in Southern California:** Southwestern California region (Transverse and northern Peninsular Ranges), western Mohave Desert, Tehachapi mountains, White and Inyo mountains; Inyo, Kern, Los Angeles, Mono, Riverside, San Bernardino, Santa Barbara, and Ventura counties. **Conservation Status:** none. **Diagnosis:** Pedicels short (<1 mm); corolla large (4-9 mm wide); nutlets 4 per fruit (2-2.5 mm long), homomorphic, and narrowly winged (wings sometimes toothed but not strongly lobed).

36. *Cryptantha costata* Brandegee (Figure 16F-K, p.36)

Common name: Ribbed/ashen cryptantha. **Distribution in Southern California:** Desert province, White and Inyo mountains, in sand dunes; Imperial, Inyo, Riverside, San Bernardino, San Diego counties. **Conservation Status:** CNPS List 4.3. **Diagnosis:** Pedicels short (<1 mm); corolla small (1-3 mm wide); nutlets 4 per fruit (1.5-2 mm long), homomorphic, narrowly winged (wings sharp, never toothed or lobed).

37. *Cryptantha inaequata* I.M. Johnst. (Figure 17A-F, p.37)

Common name: Panamint cryptantha. **Distribution in Southern California:** Mohave Desert, especially eastern; Imperial, Inyo, Riverside, San Bernardino counties. **Conservation Status:** none. **Diagnosis:** Pedicels short (<1 mm); nutlets 4 per fruit, tuberculate-papillate, rimmed to narrowly winged (wings sharp, never toothed or lobed), heteromorphic by size, 1 slightly larger than the other 3.

38. *Cryptantha angustifolia* (Torrey) Greene (Figure 17G-K, p.37)

Common name: Narrow-leaved cryptantha. **Distribution in Southern California:** Desert province; Imperial, Inyo, Riverside, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Pedicels short (<1 mm); nutlets 4 per fruit, tuberculate-papillate, margin usually rounded (rarely rimmed to narrowly winged, wings sharp, never toothed or lobed), usually heteromorphic by size, 1 slightly larger than the other 3 (rarely homomorphic). In addition to variation in nutlet morphology in this species, two forms have been noted that vary in corolla limb width and trichome density (personal communication).

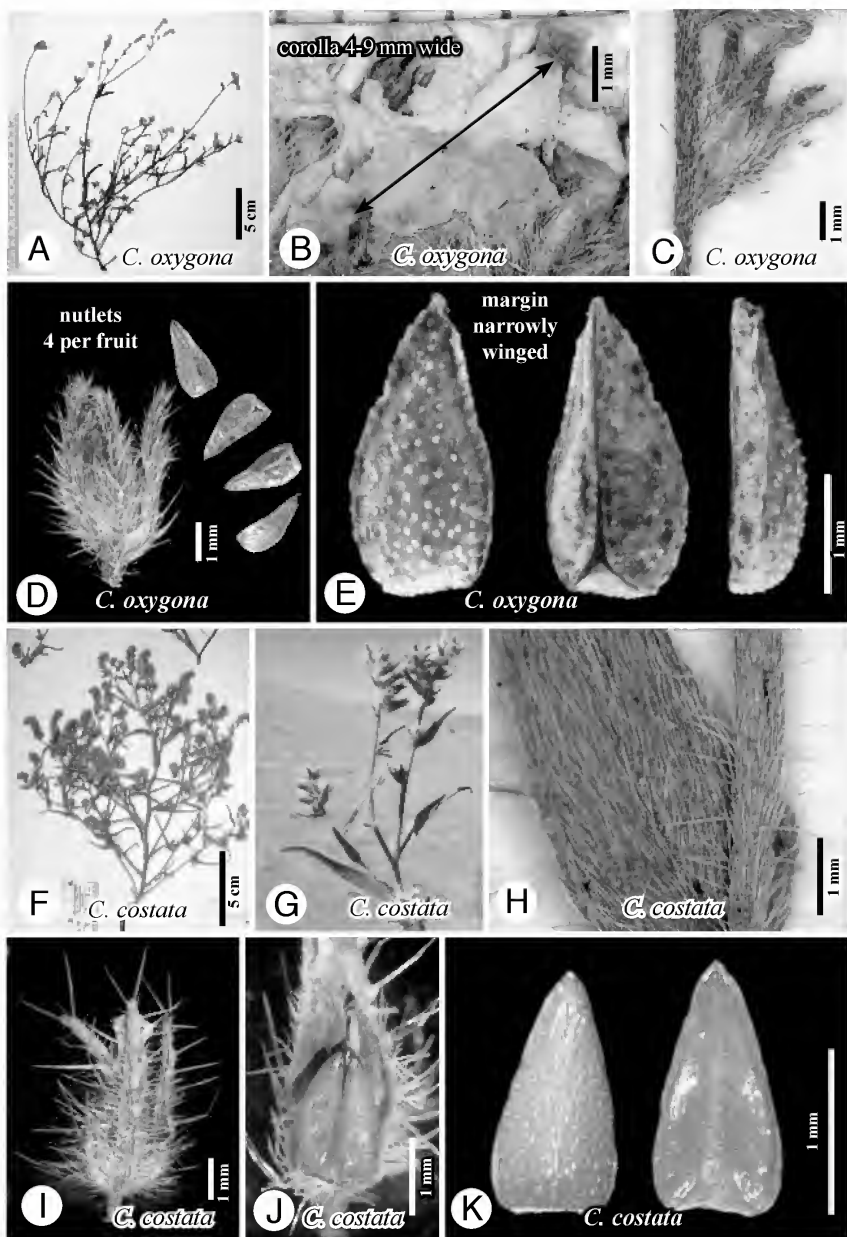


Figure 16. A-E: *Cryptantha oxygona*. **A:** Whole plant from specimen. **B:** Flower, showing relatively wide corolla. **C:** Fruit. **D:** Fruit, with 4, homomorphic nutlets removed. **E:** Nutlet, dorsal, ventral, and side views (left to right). Note narrow, toothed wing. **F-K: *Cryptantha costata*.** **F:** Whole plant from specimen. **G:** Plant in field. Note large, lanceolate inflorescence bracts. **H:** Close-up of leaf (left) and stem (right). **I:** Fruit. **J:** Fruit with sepals removed, showing four nutlets. **K:** Nutlet, dorsal (left) and ventral (right) views.

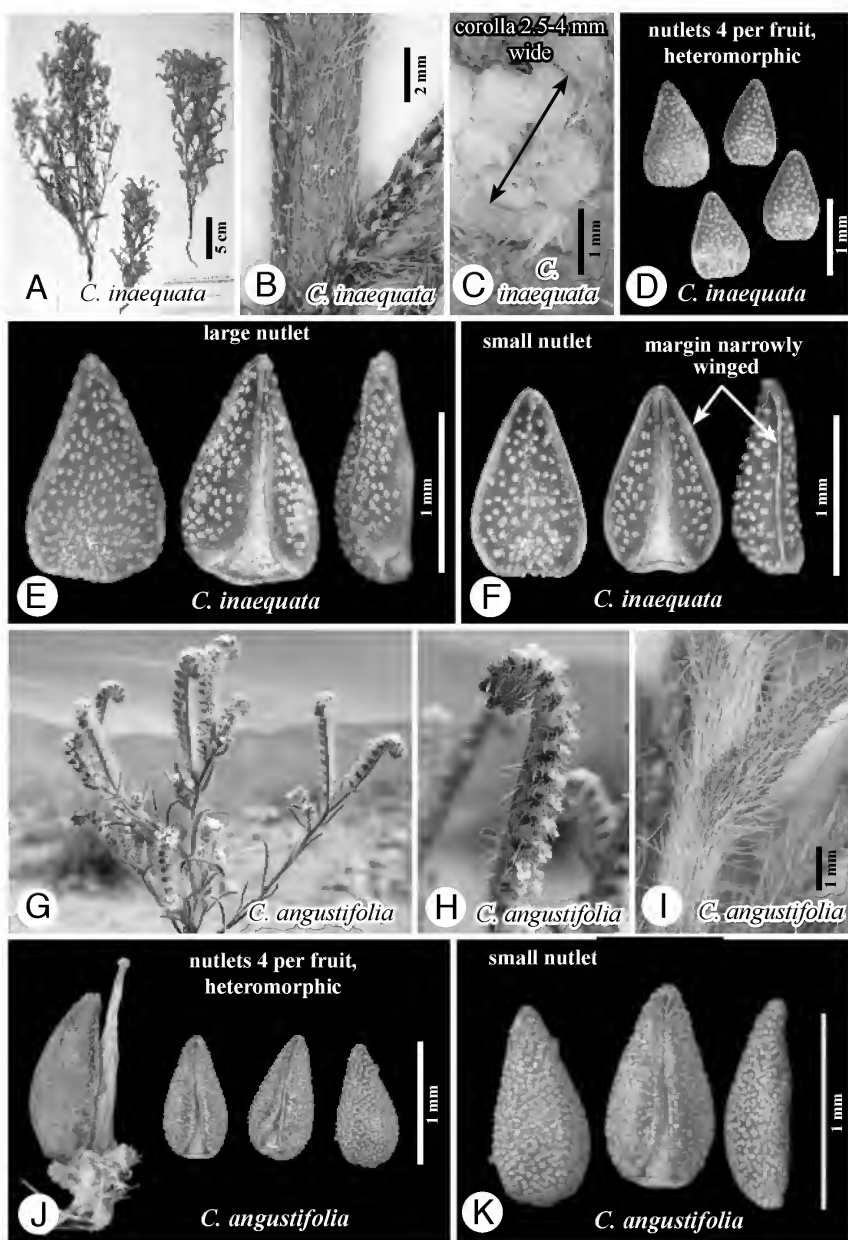


Figure 17. A-F: *Cryptantha inaequata*. **A:** Whole plants from specimen. **B:** Close-up of stem (left) and leaf (right). **C:** Flower, showing wide corolla limb. **D:** Heteromorphic nutlets, one larger. **E:** Large nutlet, dorsal, ventral, and side views (left to right). **F:** Small nutlet, dorsal, ventral, and side views (left to right). Note ovate-triangular shape and narrow wing. **G-K: *C. angustifolia*.** **G:** Whole plant in field. **H:** Inflorescence close-up. **I:** Close-up of stem (left) and leaf (right). **J:** Nutlets of one fruit, showing size heteromorphism. Note larger nutlet adherent to gynobase. **K:** Small nutlet, dorsal, ventral, and side views (left to right).

39. *Cryptantha dumetorum* (A. Gray) Greene (Figure 18A-G, p.39)

Common name: Bush-loving cryptantha. **Distribution in Southern California:** Desert province, Southwestern California region (northern Transverse Ranges); Inyo, Kern, Los Angeles, Riverside, San Bernardino counties. **Conservation Status:** none. **Diagnosis:** Stem habit sprawling, usually climbing in shrubs, foliage very green; nutlets long (2-2.5 mm), lanceolate to lance-ovate, tuberculate-papillate, heteromorphic by size (1 larger, 3 smaller) with a wide ventral groove.

40. *Cryptantha micromeres* (A. Gray) Greene (Figure 18H-M, p.39)

Common name: Minute-flowered cryptantha. **Distribution in Southern California:** Southwestern California region (South Coast, Channel Islands, Peninsular Ranges, and Transverse Ranges); Los Angeles, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Calyx sub-globose with hooked trichomes, 1-1.5 mm long; nutlets small (<1 mm long), heteromorphic, 1 large and smooth to mostly smooth, 3 smaller and tuberculate-papillate.

41. *Cryptantha recurvata* Coville (Figure 19D-E, p.40)

Common name: Bent-nut cryptantha. **Distribution in Southern California:** Desert province (Mohave, rare in Sonoran), White and Inyo mountains; Inyo, Mono, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Nutlet 1 (-2) per fruit, strongly recurved from stem, recurved in fruit at maturity, round-margined, lanceolate, and tuberculate-papillate.

42. *Cryptantha decipiens* (M.E. Jones) A.A. Heller (Figure 19F-H, p.40)

Common name: Gravel cryptantha. **Distribution in Southern California:** Desert province, White and Inyo mountains; Imperial, Inyo, Kern, Los Angeles, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Corolla small (1-1.5 mm); nutlet 1 (-2) per fruit, not recurved from stem at maturity, straight, round-margined, lanceolate, and tuberculate-papillate.

43. *Cryptantha corollata* (I.M. Johnst.) I.M. Johnst. (Figure 20A-B, p.41)

Common name: Coast range cryptantha. **Distribution in Southern California:** Southwestern California region (Transverse Ranges, northern Peninsular Ranges), Tehachapi mountains; Los Angeles, Riverside, San Bernardino, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Corolla relatively large (3-5 mm); nutlet 1 (-2) per fruit, not recurved from stem at maturity, straight, round-margined, lanceolate, and tuberculate-papillate. [*C. decipiens* (M.E. Jones) A.A. Heller *in part*, sensu W.A. Kelley and Wilken 1993]

44. *Cryptantha nevadensis* A. Nels. & P.B. Kennedy var. *nevadensis*

(Figure 20C-H, p.41)

Common name: Nevada cryptantha. **Distribution in Southern California:** Desert province, Tehachapi mountains, Southwestern California region (Transverse and Peninsular Ranges), White and Inyo mountains; Imperial, Inyo, Kern, Los Angeles, Mono, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Secondary branches sprawling, tending

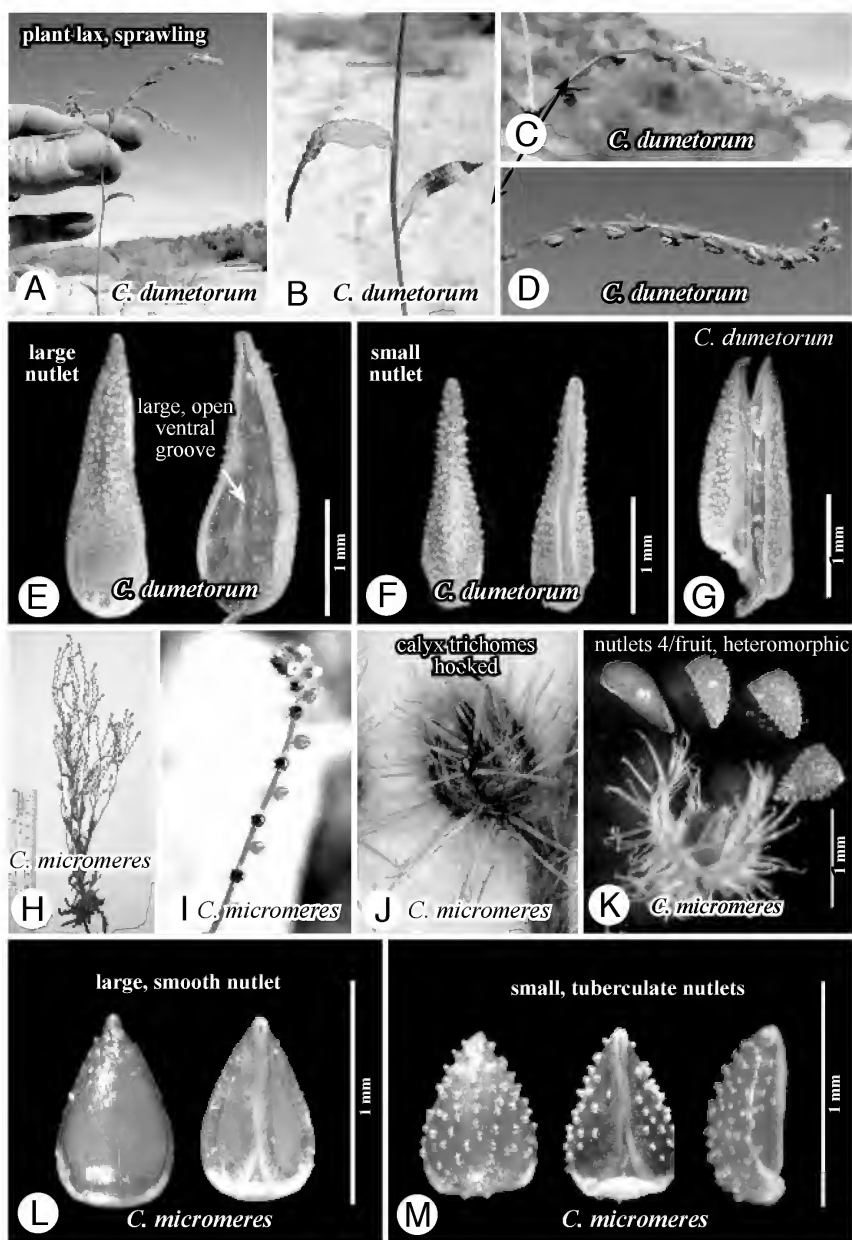


Figure 18. A-G: *Cryptantha dumetorum*. **A:** Apical shoot of plant, from field. Stem is sprawling. **B:** Stem and leaf close-up. **C-D:** Inflorescences. Note appressed flowers and fruits. **E:** Large nutlet, dorsal (left) and ventral (right) views. Note large, open ventral groove. **F:** Small nutlet, dorsal (left) and ventral (right) views. **G:** Two of four nutlets (small at left, large at right) still attached to gynobase. **H-M: *C. micromeres*.** **H:** Whole plant, from specimen. **I:** Inflorescence. **J:** Fruit, showing ovoid calyx and hooked trichomes. **K:** Fruit with four nutlets removed. Note heteromorphism. **L:** Large, mostly smooth nutlet, dorsal (left) and ventral (right) views. **M:** Small, tuberculate nutlet, dorsal, ventral, and side views.

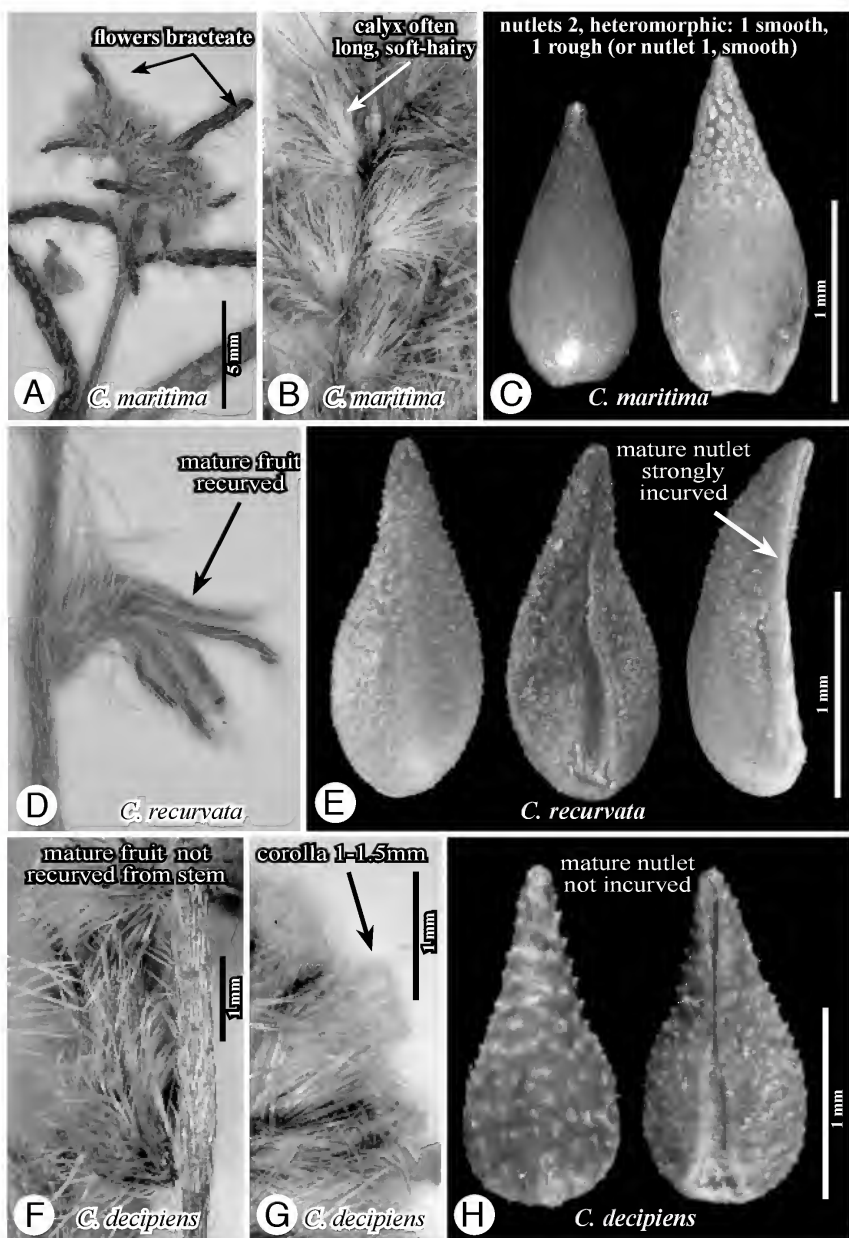


Figure 19. A-C: *Cryptantha maritima*. **A:** Inflorescence, showing bracteate flowers. **B:** Close-up of flowers and fruits. Note dense, straight trichomes. **C:** Heteromorphic nutlets, dorsal view, smooth (left) and apically rough (right). **D-E: *C. recurvata*.** **D:** Fruit, showing recurved calyx. **E:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views. Note recurved apex. **F-H: *C. decipiens*.** **F:** Fruit, ascending to inclined (not recurved). **G:** Flower, showing small corolla. **H:** Nutlet, dorsal (left) and ventral (right) views.

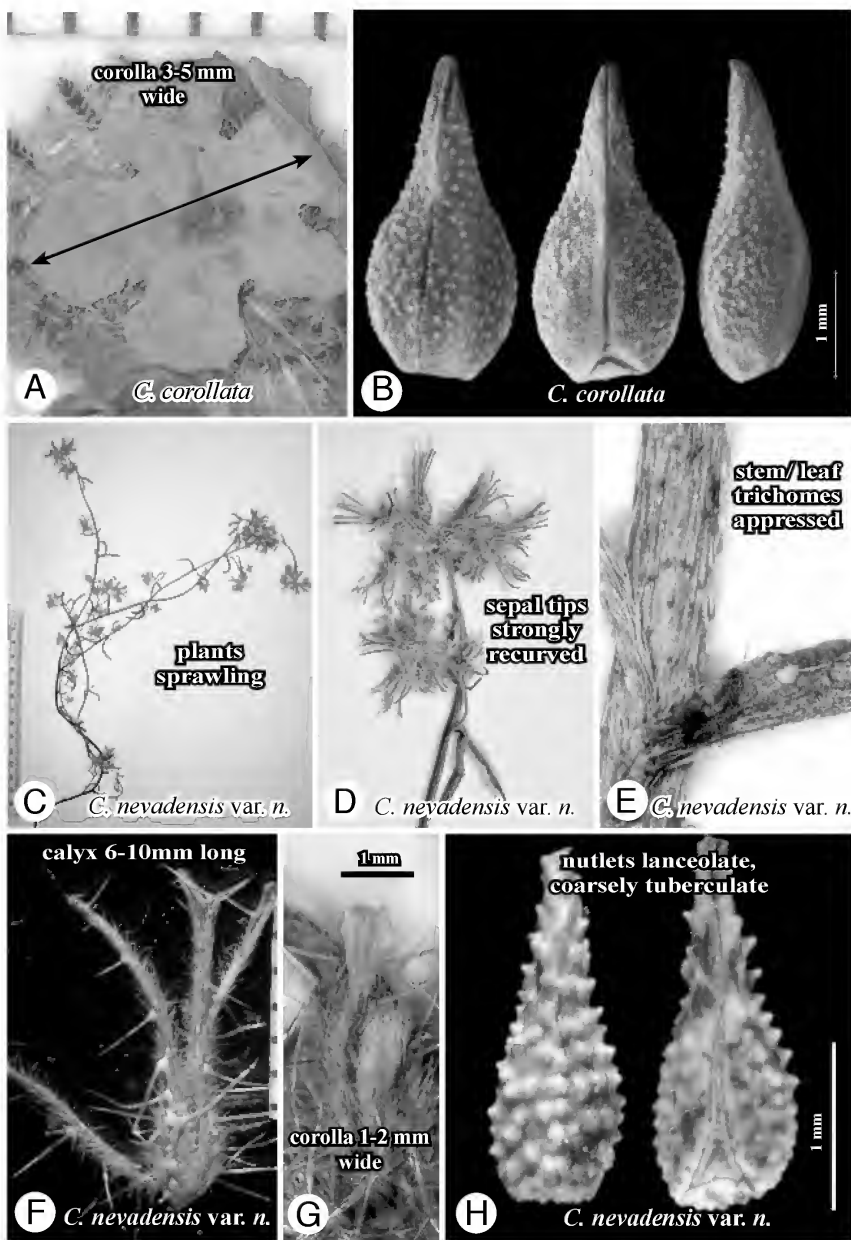


Figure 20. A-B: *Cryptantha corollata*. **A:** Flower, showing large corolla. **B:** Nutlet close-up, dorsal, ventral, and lateral views. Note relatively straight apex. **C-H: *C. nevadensis* var. *nevadensis*.** **C:** Herbarium specimen, showing sprawling stem habit. **D:** Inflorescence, showing strongly recurved sepal tips. **E:** Close-up of stem (left) and leaf (lower right). **F:** Calyx of fruit. Note long length. **G:** Flower, showing small (1-2 mm wide) corolla limb. **H:** Nutlet close-up, dorsal (left) and ventral (right) views. Note coarse tuberculation.

to crawl through shrubs; calyx relatively long (6-10 mm) with strongly recurved tips; corolla small (1-2 mm wide); nutlets round-margined, lanceolate, 4 per fruit, straight, coarsely tuberculate.

45. *Cryptantha nevadensis* A. Nels. & P.B. Kennedy var. *rigida* I.M. Johnst.

(Figure 21A-E, p.43)

Common name: Rigid cryptantha. **Distribution in Southern California:** Tehachapi mountains, Mohave Desert, Southwestern California region (Transverse and Peninsular Ranges), brushy slopes along the edge of the desert; Inyo, Kern, Los Angeles, San Bernardino, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Plant +/- erect and self supporting, with ascending secondary branches; calyx with erect to slightly recurved tips; corolla limb larger (2-4 mm wide). [*C. nevadensis* A. Nels. & P.B. Kennedy *in part*, sensu W.A. Kelley and Wilken 1993]

46. *Cryptantha scoparia* Nelson

(Figure 21F-H, p.43)

Common name: Great Basin cryptantha. **Distribution in Southern California:** White and Inyo mountains; Inyo, Mono counties. **Conservation Status:** CNPS List 4.3. **Diagnosis:** Calyx smaller (4-6 mm) and round-margined; nutlets lanceolate, 4 per fruit, straight, finely tuberculate-spinulose. [*C. nevadensis* A. Nels. & P.B. Kennedy *in part*, sensu W.A. Kelley and Wilken 1993]

47. *Cryptantha muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. var. *jonesii* (A. Gray) I.M. Johnst.

(Figure 22A, 22D-F, p.44)

Common name: Jones's cryptantha. **Distribution in Southern California:** Southwestern California region (South Coast, Transverse and Peninsular Ranges); Los Angeles, Orange, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Corolla smaller (1-2.5 mm); nutlets brownish; stems with a relatively large primary axis bearing many short, flower-bearing branchlets, forming an elongate, leafy, thyrse inflorescence. [*C. muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. *in part*, sensu W.A. Kelley and Wilken 1993]

48. *Cryptantha muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. var. *denticulata*

(Greene) I.M. Johnst.

(Figure 22B, p.44)

Common name: Prickly-nut cryptantha. **Distribution in Southern California:** Southwestern California region (Transverse and Peninsular Ranges); Los Angeles, Riverside, San Bernardino, San Diego counties. **Conservation Status:** none. **Diagnosis:** Nutlets ovate to triangular-ovate, muricate, with at least a faint median ridge on the dorsal surface. This variety is distinguished from the others by the smaller (1-2.5 mm) corolla, brownish nutlets, and stems that are loosely and sparsely branched, without a large, primary axis. [*C. muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. *in part*, sensu W.A. Kelley and Wilken 1993]

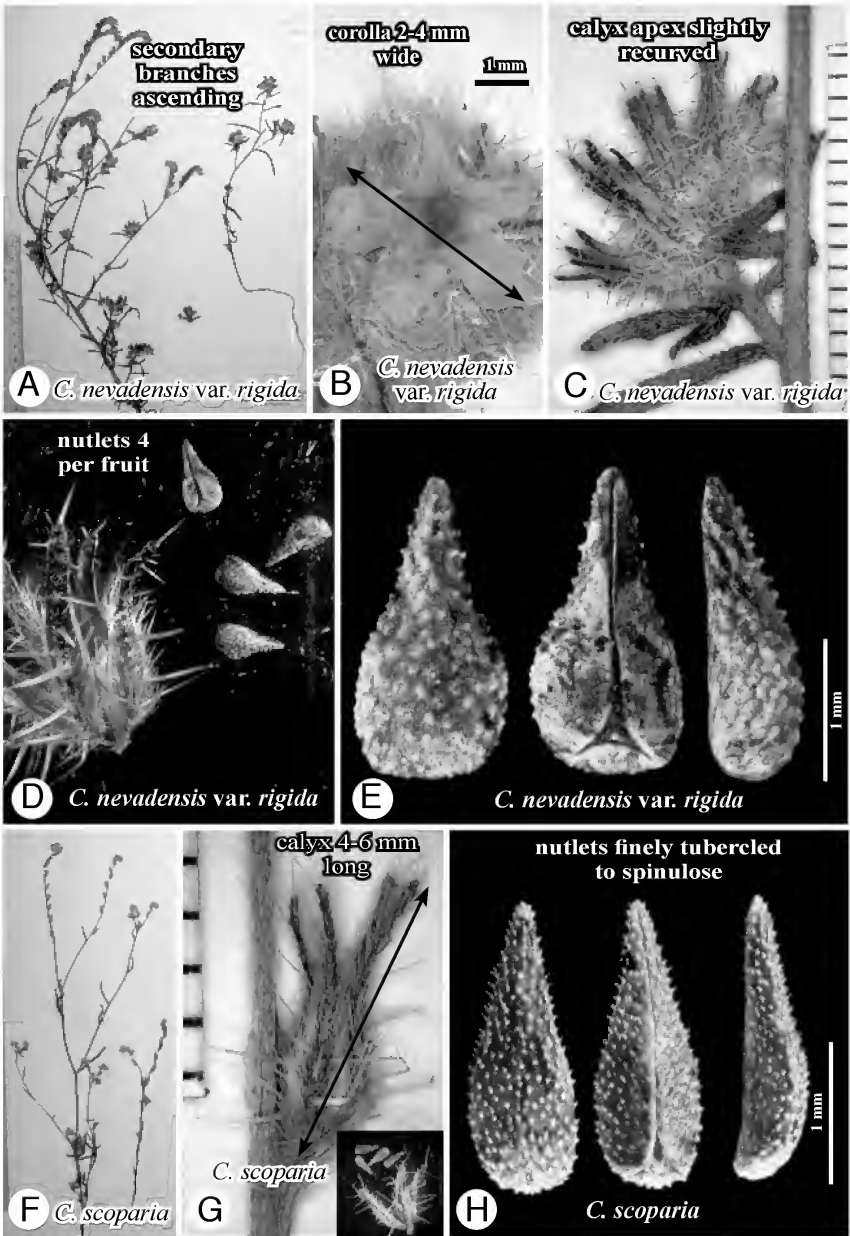


Figure 21. A-E: *Cryptantha nevadensis* var. *rigida*. **A:** Herbarium specimen. **B:** Flower close-up, showing corolla (2-4 mm wide). **C:** Inflorescence with fruits. Note long calyx with slightly recurved sepal tips. **D:** Fruit, with 4 nutlets removed. **E:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views. **F-H: *Cryptantha scoparia*.** **F:** Herbarium specimen. **G:** Fruit, showing smaller calyx. **H:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views.

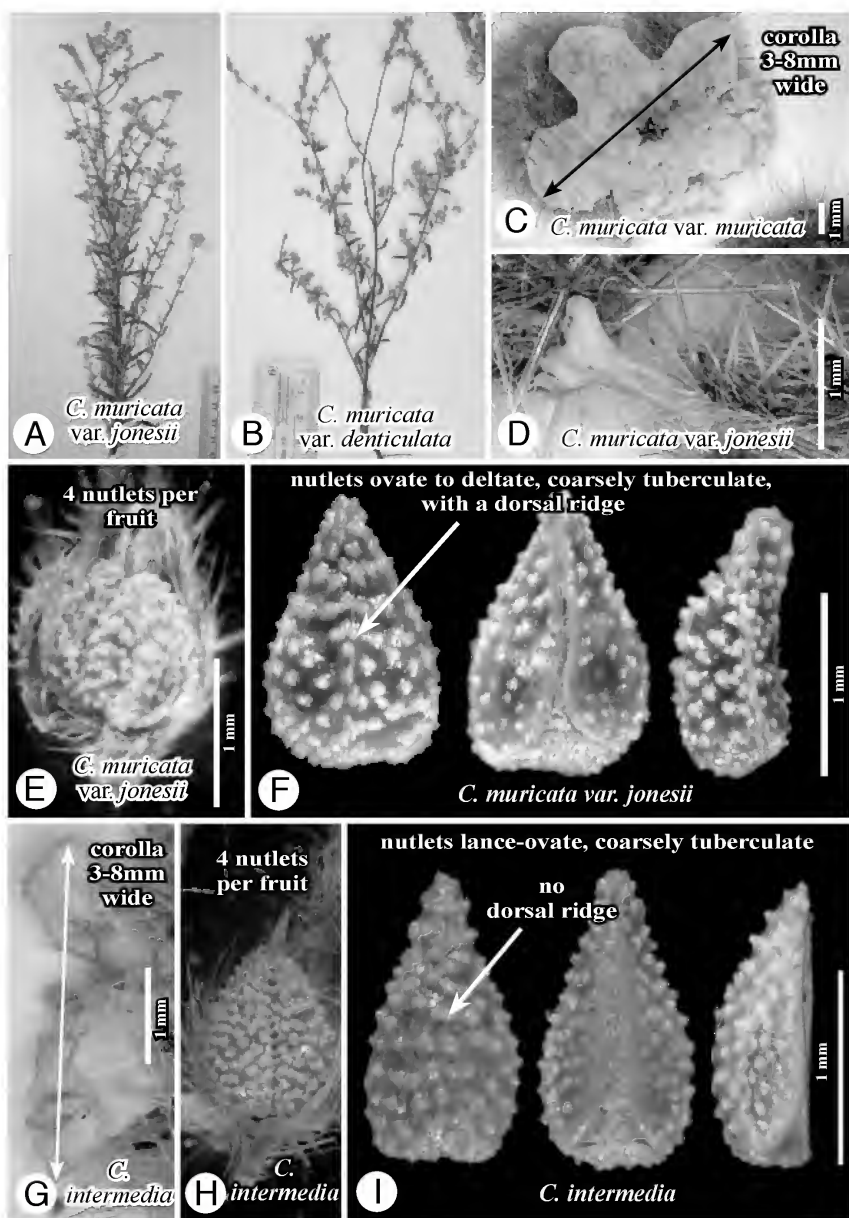


Figure 22. A-F: *Cryptantha muricata*. **A:** *C. muricata* var. *jonesii*. Herbarium specimen, showing erect, primary axis bearing numerous lateral inflorescences. **B:** *C. muricata* var. *denticulata*. Herbarium specimen, showing numerous ascending secondary branches and absence of strong primary axis. **C:** *C. muricata* var. *jonesii*. Flower close-up, showing large corolla. **D-F:** *C. muricata* var. *jonesii*. **D:** Corolla, small. **E:** Fruit, with 4 attached nutlets. **F:** Nutlet close-up, dorsal, ventral, and lateral views. Note ovate shape and dorsal ridge. **G-I: *Cryptantha intermedia* var. *intermedia*.** **G:** Flower with large corolla. **H:** Fruit, sepals removed, showing four nutlets. **I:** Nutlet close-up, dorsal, ventral, and lateral views. Note absence of dorsal ridge.

49. *Cryptantha muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. var. *muricata* (Figure 22C, p.44)

Common name: Showy prickly cryptantha. **Distribution in Southern California:** Southwestern California region (Transverse and Peninsular Ranges); Imperial, Kern, Los Angeles, Orange, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** This variety is distinguished from the others by the wider (3-8 mm) corolla and grayish nutlets.

50. *Cryptantha intermedia* (A. Gray) Greene var. *intermedia* (Figure 22G-I, p.44)

Common name: Common/Nievas cryptantha. **Distribution in Southern California:** Southwestern California region (South Coast, Channel Islands - San Clemente and Santa Catalina Islands, Transverse and Peninsular Ranges); Imperial, Inyo, Kern, Los Angeles, Orange, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Corolla relatively wide (3-6 mm), showy; nutlets 4 per fruit, homomorphic, round-margined, lance-ovate to ovate, tuberculate, lacking a dorsal ridge. **Note:** *C. intermedia* var. *grandiflora* [= *C. hendersonii* (Nelson) Piper], not native to Southern California, has much larger corollas.

51. *Cryptantha barbiger*a (A. Gray) Greene var. *ferguson*iae J.F. Macbr. (Figure 23A-E, p.46)

Common name: Palm Springs cryptantha. **Distribution in Southern California:** western Colorado Desert, especially Coachella Valley; Imperial, Riverside, San Bernardino San Diego counties. **Conservation Status:** none. **Diagnosis:** This variety is largely limited in distribution to the Coachella Valley and periphery. It is distinguished from *C. intermedia* by the significantly larger (4-6 mm in flower, 5-10 mm in fruit) calyx and from *C. barbiger*a var. *barbiger*a by the larger (4-9 mm wide) corolla. [*C. barbiger*a (A. Gray) Greene *in part*, sensu W.A. Kelley and Wilken 1993]

52. *Cryptantha trask*iae I.M. Johnst. (Figure 23F-H, p.46)

Common name: Trask's cryptantha. **Distribution in Southern California:** Southwestern California region (Channel Islands - San Clemente, San Nicolas Islands); Los Angeles, Ventura counties. **Conservation Status:** CNPS List 1B.2. **Diagnosis:** Corolla small (1-2 mm wide), nutlets round-margined, lance-ovate to ovate, tuberculate, 1-1.5(1.8) mm long, lacking a dorsal ridge.

53. *Cryptantha simulans* Greene (Figure 24A-C, p.47)

Common name: Pine cryptantha. **Distribution in Southern California:** Southwestern California region (Transverse and Peninsular Ranges); Kern, Los Angeles, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Corolla small (1-2 mm wide); nutlets 4 per fruit, round-margined, ovate with dorsal face flattened to low-convex, densely papillate - sparsely tuberculate, ca. 2 mm long, lacking a dorsal ridge.

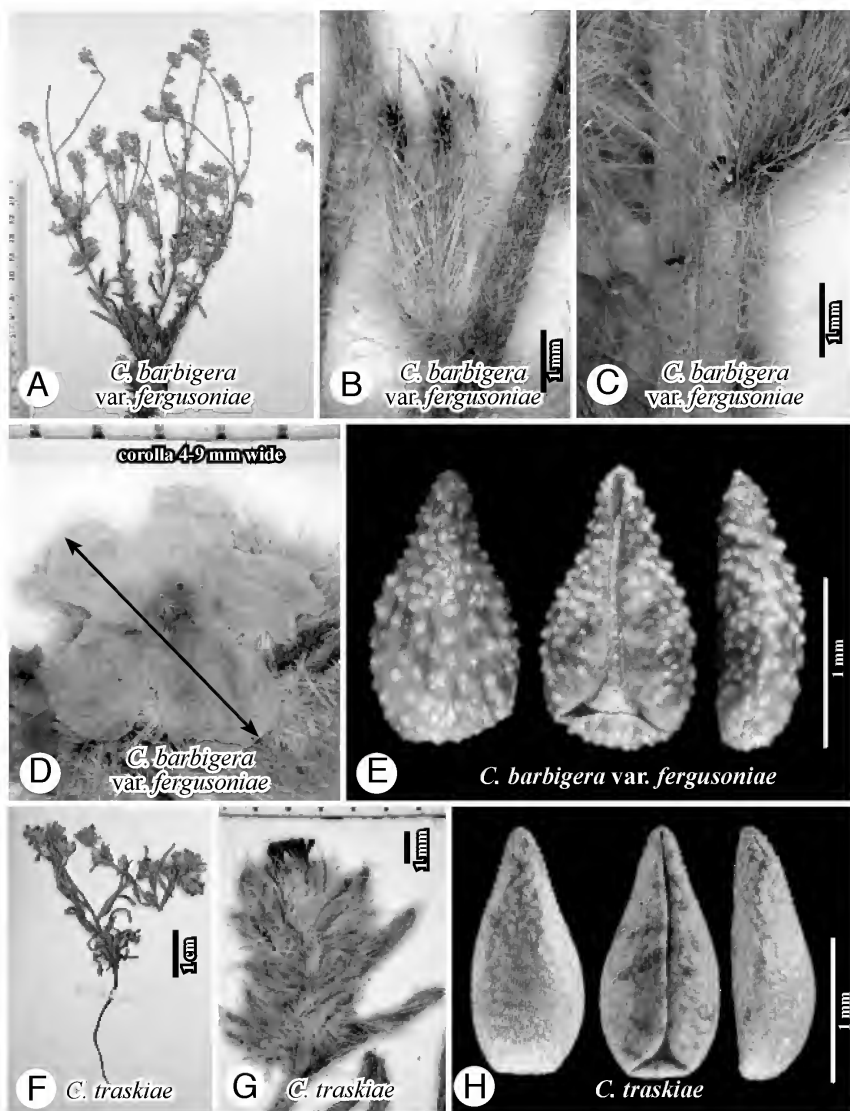


Figure 23. A-E: *Cryptantha barbigera* var. *fergusoniae*. **A:** Whole plant from herbarium sheet. **B:** Fruit. **C:** Close-up of stem (center) and leaf (upper right). **D:** Flower, showing large corolla. **E:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views. **F-H: *C. traskiae*.** **F:** Whole plant from herbarium specimen, showing short plant stature. **G:** Inflorescence. **H:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views.

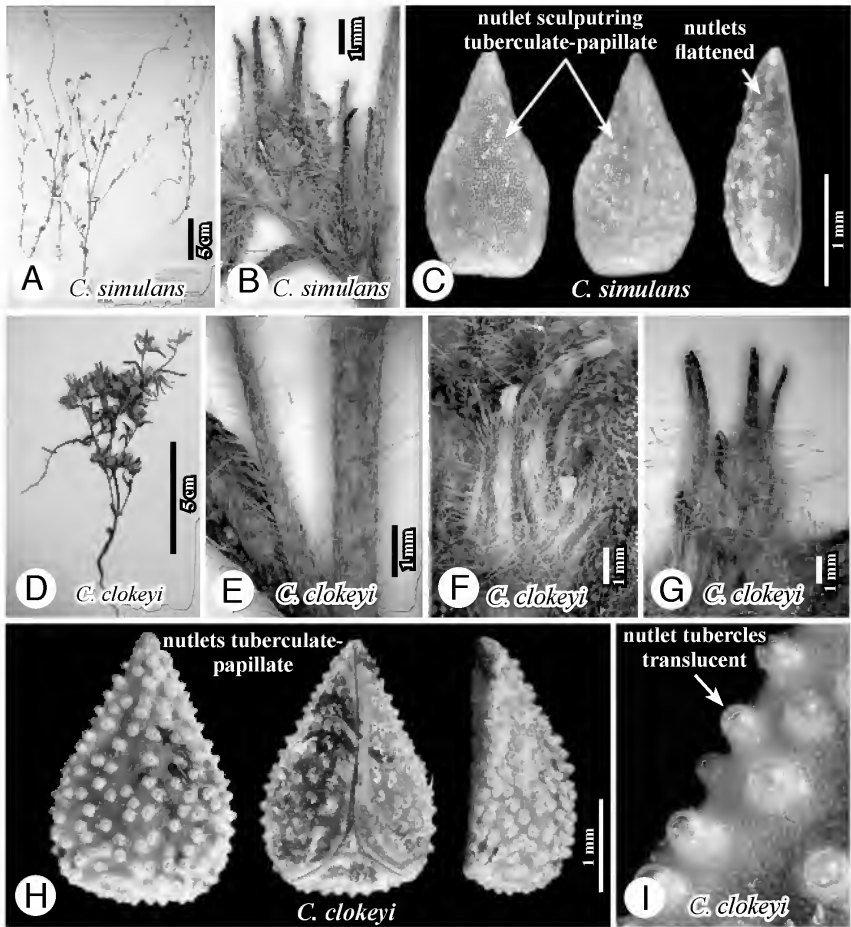


Figure 24. A-C: *Cryptantha simulans*. **A:** Whole plants from herbarium specimens. **B:** Fruit close-up. **C:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views. **D-I: *Cryptantha clokeyi*.** **D:** Whole plant from herbarium sheet. **E:** Close-up of stem (right) and leaf (far left). **F:** Flower close-up. Note small corolla. **G:** Fruit. **H:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views. **I:** Nutlet close-up, showing rounded, translucent tubercles.

54. *Cryptantha clokeyi* I.M. Johnst.

(Figure 24D-I, p.47)

Common name: Clokey's cryptantha. **Distribution in Southern California:** Mohave Desert; Inyo, Los Angeles, San Bernardino counties. **Conservation Status:** CNPS List 1B.1. **Diagnosis:** Corolla small (1-2 mm wide); nutlets 4 per fruit, ca. 3 mm long, round-margined, ovate, densely tuberculate with tubercle tips translucent, lacking a dorsal ridge.

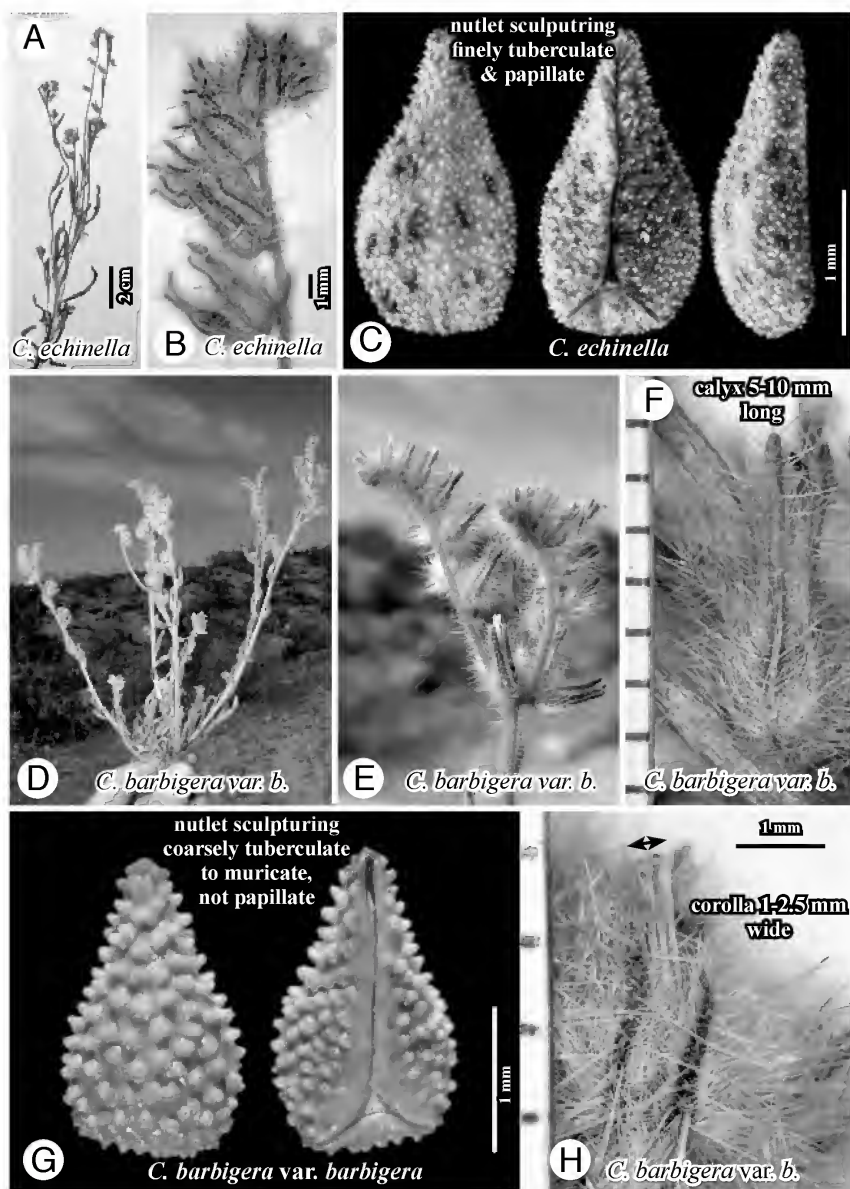


Figure 25. **A-C:** *Cryptantha echinella*. **A:** Whole plant from herbarium specimen. **B:** Inflorescence. **C:** Nutlet close-up, dorsal (left), ventral (middle), and lateral (right) views. **D-H:** *C. barbigeri* var. *barbigeri*. **D:** Whole plant in field. **E:** Inflorescence close-up. Note small corollas. **F:** Fruit, showing long calyx. **G:** Nutlet close-up, dorsal (left) and ventral (right) views. **H:** Flower, showing small corolla.

55. *Cryptantha echinella* Greene

(Figure 25A-C, p.48)

Common name: Spiny cryptantha. **Distribution in Southern California:** Tehachapi mountains, Southwestern California region (Transverse Ranges), Mohave Desert; Inyo, Kern, Los Angeles, Mono, San Bernardino, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Calyx 5-6 mm long in fruit; corolla small (1-1.5 mm wide); nutlets 4 per fruit, ca. 1.5-2 mm long, round-margined, ovate, finely tuberculate and papillate, lacking a dorsal ridge.

56. *Cryptantha barbiger* (A. Gray) Greene var. *barbiger*

(Figure 25D-H, p.48)

Common name: Bearded cryptantha. **Distribution in Southern California:** Desert province, Tehachapi mountains; Imperial, Inyo, Kern, Los Angeles, Riverside, San Bernardino, San Diego, Santa Barbara, Ventura counties. **Conservation Status:** none. **Diagnosis:** Calyx in fruit long (5-10 mm); nutlets 1-4 per fruit, 1.5-2 mm long, round-margined, ovate, densely tuberculate-muricate, lacking a dorsal ridge. This variety is distinguished from *C. b.* var. *fergusoniae* by the relatively small corolla (1-2.5 mm wide). [*C. barbiger*, in part, sensu W.A. Kelley and Wilken 1993]

NUTLET COMPARISON WITHIN MAJOR GROUPS

For comparison of nutlets within major groups, see Figures 26-30 (at end of article) for images of all Southern California *Cryptantha* taxa, arranged as follows: *Oreocarya* Group (Figure 26), *Krynitzkia* Group, smooth nutlets (Figure 27), *Krynitzkia* Group, nutlets with ridged or winged margin (Figure 28), *Greeneocharis* Group (Figure 29A,B), *Eremocarya* Group (Figure 29C,D), *Krynitzkia* Group, heteromorphic nutlets with rounded margin (Figure 29 E-H), *Krynitzkia* Group, rough nutlets with rounded or sharp-angled margin (Figure 30).

CONSERVATION STATUS AND ECOLOGY OF SOUTHERN CALIFORNIA CRYPTANTHA

Nine species of Southern California *Cryptantha* are included in the 2009 California Native Plant Society (CNPS) Inventory as sensitive or rare taxa. Of these, two species, *Cryptantha clokeyi* and *C. ganderi*, are on CNPS List **1B.1**, which signifies that they are “rare, threatened, or endangered in California and elsewhere” and “seriously endangered in California (over 80% of occurrences threatened/high degree and immediacy of threat).” *Cryptantha clokeyi* is found in “sandy or gravelly soil” (R.B. Kelley *in prep*) in the Mohave Desert region, in three counties (Inyo, Los Angeles, and San Bernardino). Only **16** original collections are cited in the *Consortium of California Herbaria* at the time of this writing. *Cryptantha ganderi* is found in “stabilized, +/- silty, fine sand deposits, creosote scrub association” (R.B. Kelley, *in prep.*), solely in parts of the Borrego Valley of San Diego County. Only **9** original collections are currently cited in the *Consortium of California Herbaria*.

Two Southern California *Cryptantha* species are on CNPS List **1B.2**, meaning “rare, threatened, or endangered in California and elsewhere” and “fairly endangered in California (20-80% occurrences threatened).” One of these, *C. roosiorum*, is a distinctive member of *Oreocarya*. It is known from “rocky, silty soils, dry meadows in open bristlecone pine-limber pine forest, limestone endemic” (R.B. Kelley, in prep.) of only three nearby localities in the Inyo Mountains (Inyo County). Only **5** original collections are cited in the *Consortium of California Herbaria*. The second CNPS List **1B.2** species is *C. traskiae*, which is found only on two of the Channel Islands: San Clemente Island (Los Angeles County) and San Nicolas Island (Ventura County), both of the southern group. However, *C. traskiae* has been collected considerably more, as **60** original collections (almost two-thirds by S. A. Junak) are cited in the *Consortium of California Herbaria*.

The five other *Cryptantha* species included in the CNPS Inventory – *C. costata*, *C. glomeriflora*, *C. holoptera*, *C. scoparia*, and *C. tumulosa* – are on List **4.3**, meaning they are relatively rare, of “limited distribution (watch list)” and are “not very endangered in California (<20% of occurrences threatened or no current threats known).”

Cryptantha taxa are found in a variety of substrate types and habitats. Most members of the *Eremocarya*, *Greeneocharis*, and *Krynitzkia* groups grow in sandy or gravel soil. *Cryptantha flavoculata*, *C. hoffmannii*, *C. humilis*, *C. roosiorum*, *C. tumulosa*, and *C. virginensis* of the *Oreocarya* group and *C. inaequata* of the *Krynitzkia* group occur occasionally or solely in limestone-based substrates. Interestingly, members of the perennial *Oreocarya* group tend to occur in high elevation, mountainous regions; the taxa in Southern California are found at elevations ranging from 840-3600 meters (2,700-11,800 feet), with a median elevation of 2,300 meters (7,700 feet). In addition, two common *Cryptantha* species – *C. flaccida* and *C. intermedia* (no variety indicated) – are cited as “weak” or “indifferent” indicators of ultramafic substrates (Safford et al. 2005).

TAXONOMIC PROBLEMS IN *CRYPTANTHA*

Several *Cryptantha* taxa of Southern California warrant further studies, both quantitative statistical studies of morphology and genetic studies at the population level. Comparative studies of biogeography, ecology, and reproductive biology of the *Greeneocharis* species pair (*C. circumscissa* and *C. similis*) are needed to better understand how they may be related to one another and how they diverged. Within the *Krynitzkia* group, the varieties of *C. clevelandii* need to be properly documented with respect to biogeographic distribution, habitat differences, and variation. *Cryptantha angustifolia* is reported to have variants, including forms with homomorphic and winged nutlets, in contrast to the typical heteromorphic, round-margined nutlets, and forms differing in corolla width and vestiture. The complex of varieties in *C. muricata* are at times difficult to identify and appear to intergrade, particularly in the southern part of the range. Additional research is needed on this group (R. B. Kelley, pers. comm. 2008). What is called *C. intermedia* var. *intermedia* shows considerable

variation in leaf morphology from coastal to montane habitats. *Cryptantha corollata* shows considerable variation. *Cryptantha maritima* might be worthy of further study with regard to variation in calyx trichome morphology, given that the synonymized *C. m.* var. *pilosa* presumably differs in that regard. Both *Cryptantha maritima* and *C. circumscissa* would be fruitful to study with respect to potential differences between populations in North versus South America and the assessment of the direction and timing of their dispersal events. In general, it is likely that many collections of *Cryptantha* across California need careful annotation, using the taxonomy and keys in the upcoming *The Jepson Manual* (R.A. Kelley, *in prep*). Just before this article went to press, we received notification of a population of *Cryptantha fendleri* (not previously known in California) collected this year in the Little Cowhorn Valley of the Inyo Mountain range, thus technically part of the Southern California region. *Cryptantha fendleri*, a member of the smooth nutlet *Krynitzkia* group, will be included in the second edition of *The Jepson Manual* (R. A. Kelley, *in prep*) and is currently being considered for CNPS List 2.3 [“rare, threatened, or endangered in California, but more common elsewhere; not very endangered in California (<20% of occurrences threatened or no current threats known)”.]. Finally, Southern California *Cryptantha* that are potentially new to science are currently being evaluated (Jim Andre, personal communication; authors of this paper), which could add even more to the Southern California region’s diversity of this fascinating group.

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We are greatly indebted to the herbaria at **COLO**, **RSA-POM**, **SD**, **SDSU**, and **UC-JEPS** for specimen loans, to all the herbaria that are members of the *Consortium of California Herbaria* (**CAS-DS**, **CDA**, **CHSC**, **DAV**, **HSC**, **IRVC**, **OBI**, **PGM**, **RSA-POM**, **SBBG**, **SD**, **SDSU**, **SJSU**, **UC-JEPS**, **UCR**, **UCSB**, and **UCSC**, as of this writing) for access to their data, and to **UC-JEPS** in particular for creating and maintaining the *Consortium* data interface. We thank Ron B. Kelley for an early version of his descriptions and keys of *Cryptantha*, to be incorporated in the second edition of *The Jepson Manual*. We thank Anna Schochenmaier for photographing several of the high resolution images of nutlets. We thank Gary Monroe for allowing us to use field images of *C. cinerea* var. *abortiva*, *C. confertiflora*, and *C. flavoculata*. We sincerely thank Andy Sanders and Leroy Gross for reviewing this paper and giving useful suggestions (but of course we take responsibility for any errors). Finally, we thank the editors of *Crossosoma* for inviting us to publish this article, which is an offshoot of a talk given at the 2008 Southern California Botanists meeting.

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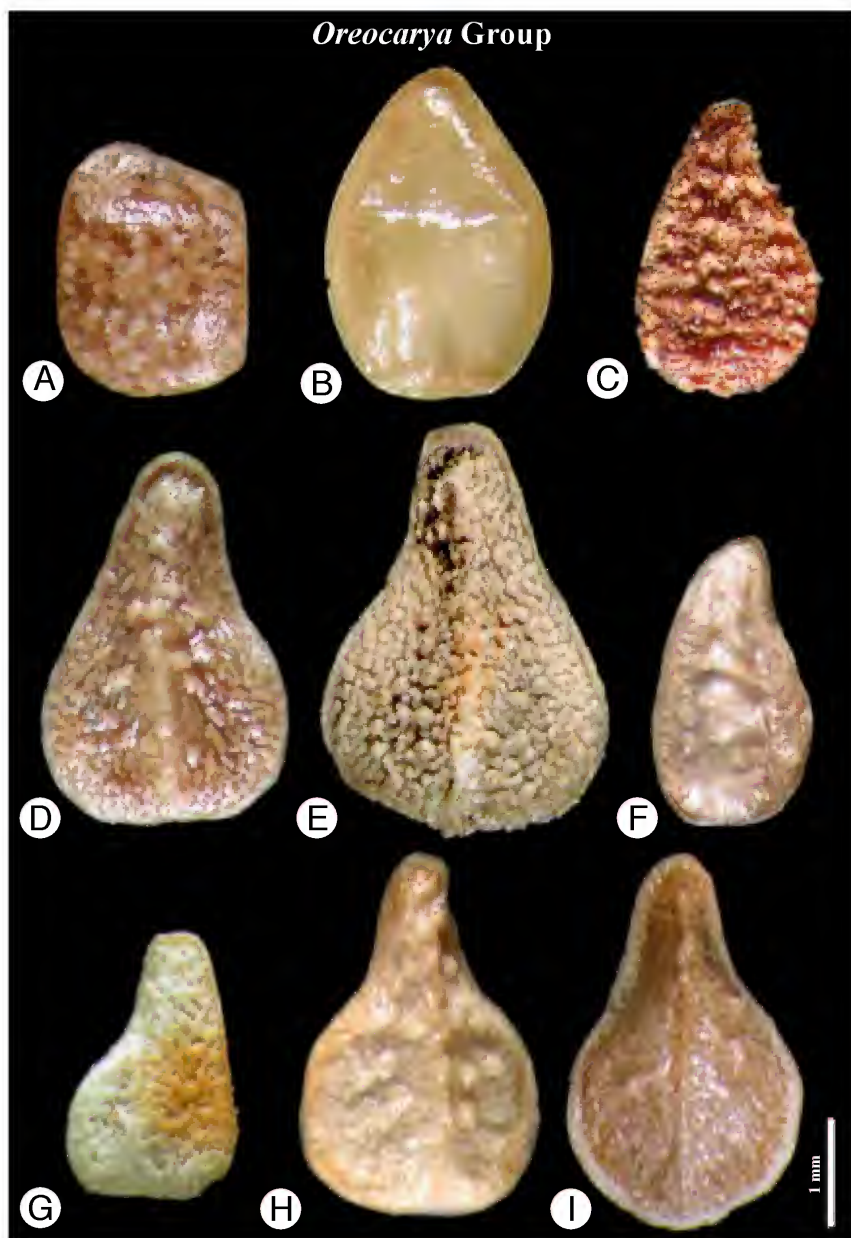


Figure 26. *Oreocarya* group nutlets (dorsal view). **A:** *Cryptantha cinerea* var. *abortiva*. **B:** *C. confertiflora*. **C:** *C. flavoculata*. **D:** *C. hoffmannii*. **E:** *C. humilis*. **F:** *C. nubigena*. **G:** *C. roosiorum*. **H:** *C. tumulosa*. **I:** *C. virginensis*. All images to scale.

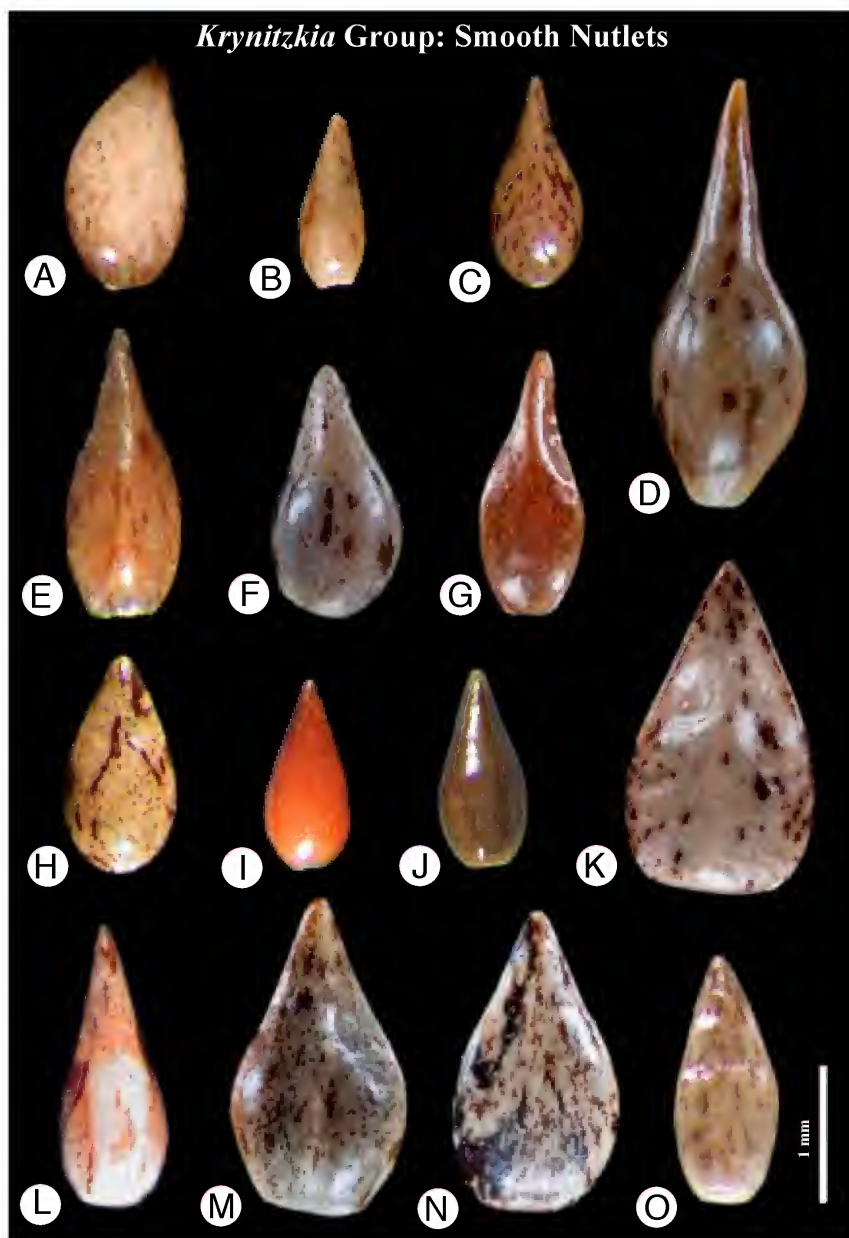


Figure 27. *Krynitzkia* group, smooth nutlets (dorsal view). **A:** *Cryptantha affinis*. **B:** *C. clevelandii* var. *clevelandii*. **C:** *C. clevelandii* var. *florosa*. **D:** *C. flaccida*. **E:** *C. ganderi*. **F:** *C. glomeriflora*. **G:** *C. gracilis*. **H:** *C. leiocarpa*. **I:** *C. maritima*. **J:** *C. microstachys*. **K:** *C. mohavensis*. **L:** *C. nemaclada*. **M:** *C. sparsiflora*. **N:** *C. torreyana*. **O:** *C. watsonii*. All images to scale.

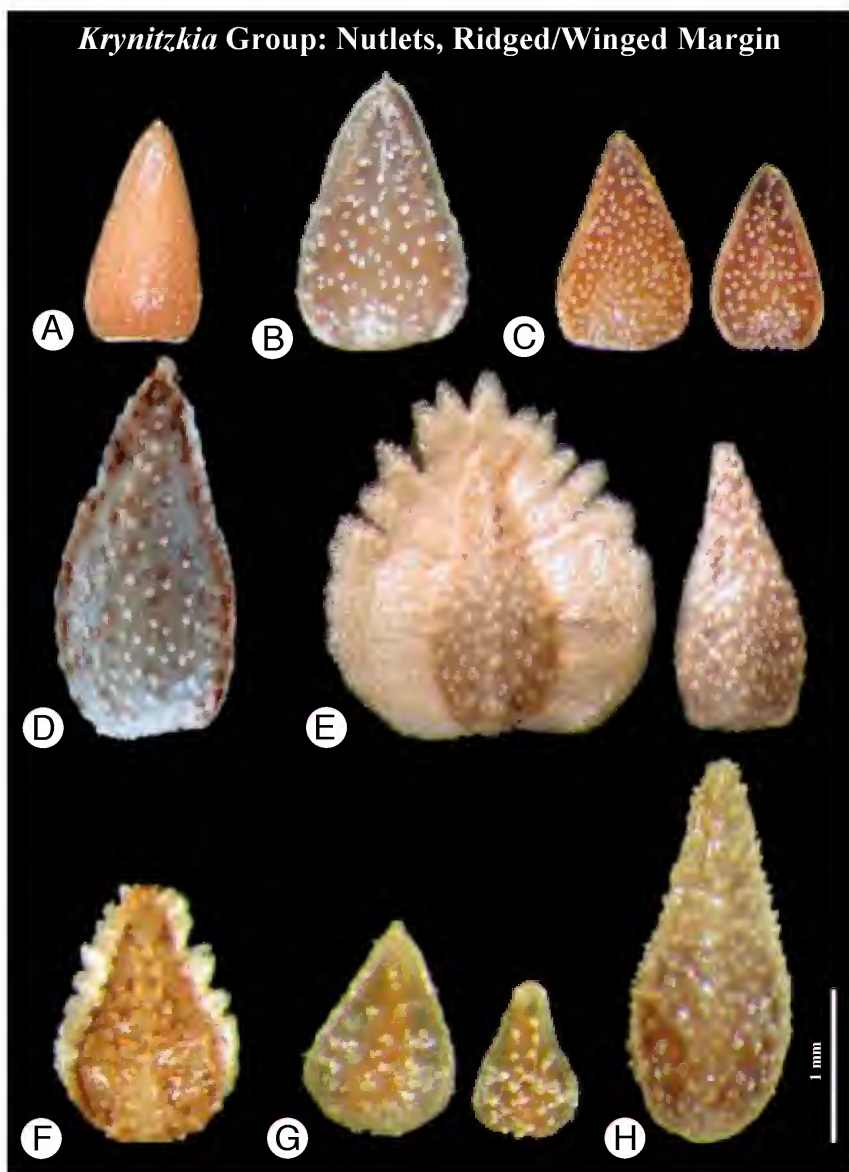


Figure 28. *Krynitzkia* group, nutlets with a ridged or winged margin (dorsal view). **A:** *Cryptantha costata*. **B:** *C. holoptera*. **C:** *C. inaequata*. **D:** *C. oxygona*. **E:** *C. pterocarya* var. *pterocarya*, winged nutlet (left), unwinged (right). **F:** *C. pterocarya* var. *purpusii*, winged nutlet. **G:** *C. racemosa*. **H:** *C. utahensis*. All images to scale.

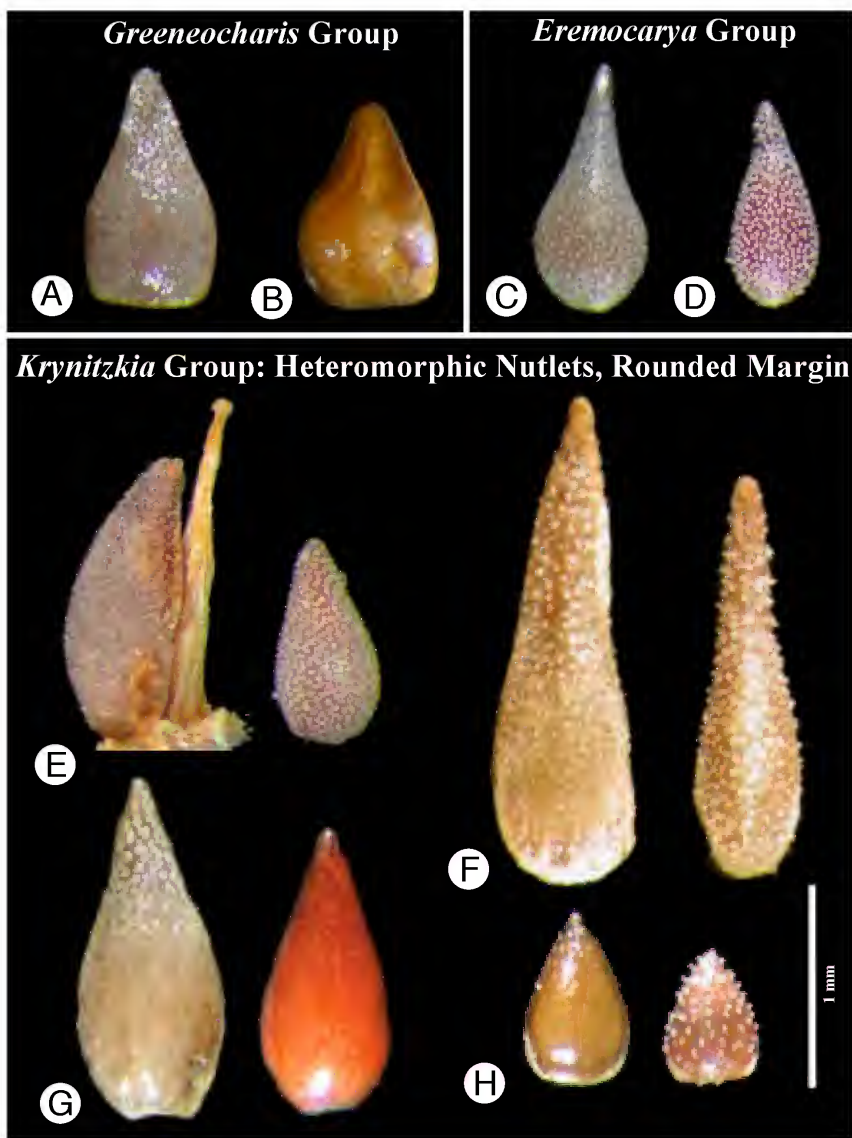


Figure 29. **A-B:** *Greeneocharis* group nutlets (dorsal view). **A:** *Cryptantha circumscissa*. **B:** *C. similis*. **C-D:** *Eremocarya* group nutlets (dorsal view). **C:** *C. lepida*. **D:** *C. micrantha*. **E-H:** *Krynitzkia* group, heteromorphic nutlets with a rounded margin (dorsal view, except large nutlet of *C. angustifolia* in lateral view). **E:** *C. angustifolia*. **F:** *C. dumetorum*. **G:** *C. maritima*. **H:** *C. micromeres*. All images to scale.

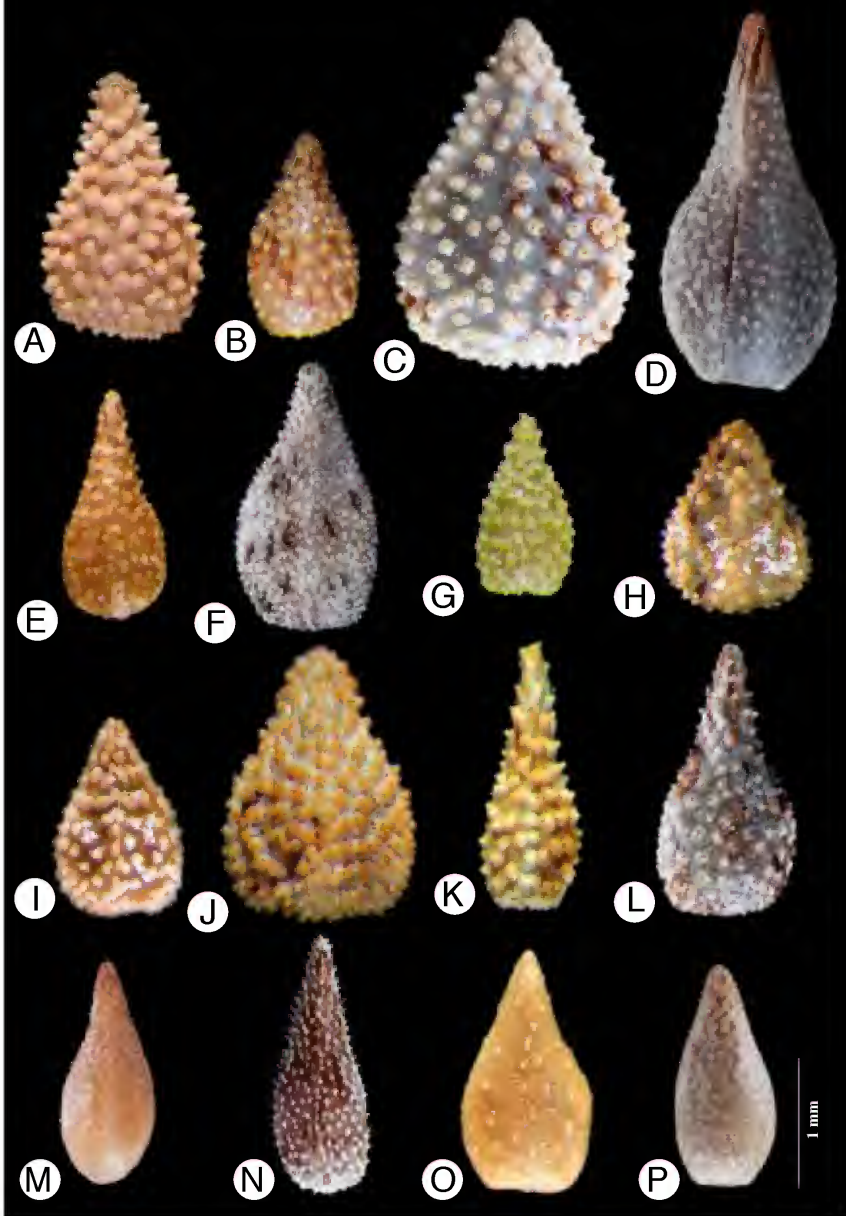
Krynitzkia Group: Rough Nutlets, Round or Sharp Margin

Figure 30. *Krynitzkia* group, rough nutlets with a rounded or sharp-angled margin (dorsal view). **A:** *Cryptantha barbiger* var. *barbiger*. **B:** *C. barbiger* var. *fergusonae*. **C:** *C. clokeyi*. **D:** *C. corollata*. **E:** *C. decipiens*. **F:** *C. echinella*. **G:** *C. intermedia* var. *intermedia*. **H:** *C. muricata* var. *denticulata*. **I:** *C. muricata* var. *jonesii*. **J:** *C. muricata* var. *muricata*. **K:** *C. nevadensis* var. *nevadensis*. **L:** *C. nevadensis* var. *rigida*. **M:** *C. recurvata*. **N:** *C. scoparia*. **O:** *C. simulans*. **P:** *C. traskiae*. All images to scale.

Appendix 1. Voucher information for *Cryptantha* specimens examined and photographed in this study.

Cryptantha affinis (A. Gray) Greene: Figure 8A, 27A (SDSU 5410); *Cryptantha angustifolia* (Torrey) Greene: Figure 17G,H (SDSU 18676), Figure 17I (SDSU 13030), Figure 17J, 29E (SDSU 5376); *Cryptantha barbigena* (A. Gray) Greene var. *barbigena*: Figure 24D,E (SDSU 18686), Figure 24F,H (SDSU 9986), Figure 24G, 30A (SDSU 5378); *Cryptantha barbigena* (A. Gray) Greene var. *fergussonae* J.F. Macbr.: Figure 25A-C,E, 30B (RSA 712692), Figure 25D (RSA 713328); *Cryptantha cinerea* (Greene) Cronquist var. *abortiva* (Greene) Cronquist: Figure 5F-H, 26A (RSA 46663); *Cryptantha circumscissa* (Hook. & Arn.) I.M. Johnston: Figure 3A,B (SDSU 18697), Figure 3C-E, 29A (SD 28881); *Cryptantha clevelandii* Greene var. *clevelandii*: Figure 10F,G (SDSU 14050), Figure 10H, 27B (SDSU 14059); *Cryptantha clevelandii* Greene var. *florosa* I.M. Johnston: Figure 11A (SDSU 18342), Figure 11B-D, 27C (SDSU 5417); *Cryptantha clokeyi* I.M. Johnston: Figure 23G-L, 30C (RSA 665270); *Cryptantha confertiflora* (Greene) Payson: Figure 5B, 26B (RSA 196047); *Cryptantha corollata* (I.M. Johnston) I.M. Johnston: Figure 20A,B, 30D (POM 368220); *Cryptantha costata* Brandegei: Figure 16F,H-J (SD 113106), Figure 16G (SDSU 17342), Figure 16K, 28A (SD 113307); *Cryptantha decipiens* (M.E. Jones) A. Heller: Figure 19F,H, 30E (SDSU 18645), Figure 19G (SDSU 16365); *Cryptantha dumetorum* (A. Gray) Greene: Figure 18A-D (SDSU 18694), Figure 18E-G, 29F (RSA 553891); *Cryptantha echinella* Greene: Figure 24A-C, 30F (RSA 682890); *Cryptantha flaccida* (Lehmann) Greene: Figure 8D (SD 120625), Figure 8E, 27D (SDSU 17311); *Cryptantha flaviculata* (A. Nels.) Payson: Figure 5D, 26C (SD 21927); *Cryptantha ganderi* I.M. Johnston: Figure 9C,D, 27E (SD 115050); *Cryptantha glomeriflora* Greene: Figure 8B, 27F (SD 87724), Figure 8C (RSA 625075); *Cryptantha gracilis* Osterh.: Figure 10A (RSA 709650), Figure 10B, 27G (SD 4205); *Cryptantha hoffmannii* I.M. Johnston: Figure 7A,C (SD 81222), Figure 7B (SDSU 5495), Figure 7D, 26D (RSA 79771); *Cryptantha holoptera* (A. Gray) J.F. Macbr.: Figure 13A,B, 28B (SD 120959), Figure 13C (SDSU 13036); *Cryptantha humilis* (A. Gray) Payson: Figure 6E (SD 87618), Figure 6F, 26E (RSA 516990); *Cryptantha inaequata* I.M. Johnston: Figure 17A-F, 28C (RSA 173141); *Cryptantha intermedia* (A. Gray) Greene var. *intermedia*: Figure 22G (SDSU 16074), Figure 22H,I, 30G (SDSU 14564); *Cryptantha leiocarpa* (Fisher & C. A. Meyer) Greene: Figure 9E,G, 27H (SDSU 19212); *Cryptantha lepida* (A. Gray) I.M. Johnston: Figure 4A-C (SDSU 17572), Figure 4D-E, 29C (SDSU 17281); *Cryptantha maritima* (Greene) Greene var. *maritima*: Figure 9F,H (SDSU; inset SD 113111), Figure 19A-C(left), 27I, 29G (right) (SD 113111), Figure 19C(right), 29G (left) (SDSU 5460); *Cryptantha micrantha* (Torrey) I.M. Johnston: Figure 4F (SDSU 5388), Figure 4G, 29D (SDSU 5421), Figure 4H,I (SDSU 5431), Figure 4J (SDSU 5419); *Cryptantha micromeres* (A. Gray) Greene: Figure 18H,J (SDSU 16695), Figure 18K (SDSU 15465), Figure 18L-M, 29H (SDSU 12173); *Cryptantha microstachys* (A. Gray) Greene: Figure 10C,D (SD 58176), Figure 10E, 27J (SD 44966); *Cryptantha mohavensis* (Greene) Greene: Figure 12A, 27K (SD 129726), Figure 12B (RSA 712528); *Cryptantha muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. var. *denticulata* (Greene) I.M. Johnston: Figure 22B, 30H (SD 161808); *Cryptantha muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. var. *jonesii* (A. Gray) I.M. Johnston: Figure 22A,E (SDSU 16714), Figure 22D (17512), Figure 22F, 30I (SDSU 5413); *Cryptantha muricata* (Hook. & Arn.) A. Nels. & J.F. Macbr. var. *muricata*: Figure 22C, 30J (SDSU 19186); *Cryptantha uemaculata* Greene: Figure 9A,B, 27L (RSA 195150); *Cryptantha nevadensis* A. Nels. & P.B. Kennedy var. *nevadensis*: Figure 20C-H, 30K (SDSU 13032); *Cryptantha nevadensis* A. Nels. & P.B. Kennedy var. *rigida* I.M. Johnston: Figure 21A-E, 30L (RSA 580318), Figure 21B (POM 287290); *Cryptantha uubigena* (Greene) Payson: Figure 6C (JEPS 90327), Figure 6D, 26F (SD 87723); *Cryptantha oxygona* (A. Gray) Greene: Figure 16A-D (RSA 717219), Figure 16E, 28D (RSA 709140); *Cryptantha pterocarya* (Torrey) Greene var. *cycloptera* (Greene) J.F. Macbr.: Figure 15C (SDSU 17298); *Cryptantha pterocarya* (Torrey) Greene var. *pterocarya*: Figure 14E (SDSU 18692), Figure 14F,G (SDSU 12435), Figure 15A, 28C (SDSU 5500), Figure 15B (SDSU 17304); *Cryptantha pterocarya* (Torrey) Greene var. *purpurea* Jeps.: Figure 15 D,E, 28F (SD 91861); *Cryptantha racemosa* (S. Watson) Greene: Figure 13D (SDSU 5494), Figure 13E,G, 28G (SD 42216), Figure 13F (SDSU 18710); *Cryptantha recurvata* Coville: Figure 19D (RSA 370268), Figure 19E, 30M (RSA 250147); *Cryptantha roosiorum* Munz: Figure 6A,B, 26G (RSA 346621); *Cryptantha scoparia* Nelson: Figure 21F,G (RSA 641530), Figure 21H, 30N (POM 170650); *Cryptantha smilii* K. Mathew & P.H. Raven: Figure 3F-I (RSA 272392), Figure 3J, 29B (RSA 660941); *Cryptantha simulans* Greene: Figure 23D,E (SD 70318), Figure 23F, 30O (SDSU 5488); *Cryptantha sparsiflora* (Greene) Greene: Figure 8F (SD 40827), Figure 8G, 27M (RSA 191197); *Cryptantha torreyana* (A. Gray) Greene: Figure 11E-I (JEPS 102382), Figure 11J, 27N (SD 129490); *Cryptantha traskiae* I.M. Johnston: Figure 23A,B (JEPS 93692), Figure 23C, 30P (SD 90374); *Cryptantha tumulosa* (Payson) Payson: Figure 7H (SD 107276), Figure 7I, 26H (SD 58351); *Cryptantha utahensis* (A. Gray) Greene: Figure 14A (SDSU 18688), Figure 14B-D, 28H (SD 100153); *Cryptantha virginensis* (M.E. Jones) Payson: Figure 7E (SD 107269), Figure 7F (SDSU 5501), Figure 7G, 26F (RSA 340713); *Cryptantha watsonii* (A. Gray) Greene: Figure 12C (COLO 503943), Figure 12D, 27O (RSA 51987).

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Front Cover:

Nutlet dorsal images of all 49 species and 56 taxa (including varieties) of *Cryptantha* in Southern California. All images to scale.